

**MARINE BENTIC ALGAE AND THE ENVIRONMENT
IN THE ØRESUND. III.**

BY

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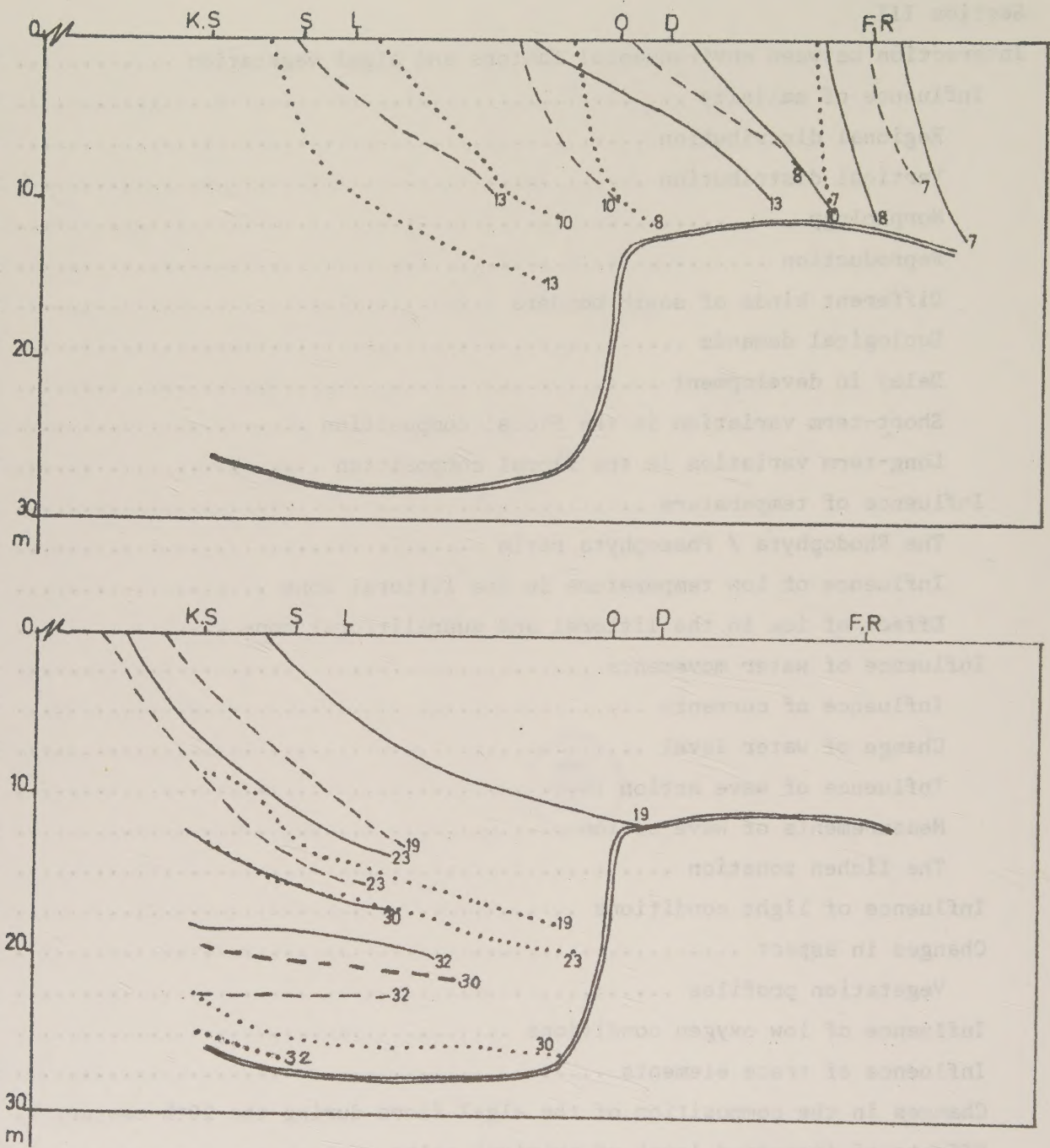


Fig. 123. Quartile values of salinity (o/oo) in relation to depth from north to south in the Öresund, based on Table 2 and own measurements.

q_1	K.S = Kattegatt South	O = Oskarsgrundet
q_2 - - - -	S = Svinbådan	D = Drogden
q_3 ———	L = Lappegrund	F.R = Falsterbo Reef

INTERACTION BETWEEN ENVIRONMENTAL FACTORS AND ALGAL VEGETATION

As has been shown in section II there are great differences in the composition of the algal flora, as well as in the morphology, reproduction and vertical distribution of the species between the northern and southern part of the Öresund. In the following section the influence of the environmental factors, described in section I, on the algal flora will be discussed. It is, however, apparent that it is very difficult to discuss one parameter separately, as the changes in the vegetation may be the result of a complex interaction of several environmental factors.

INFLUENCE OF SALINITY

The salinity conditions in the Öresund area are extremely complex with an unstable gradient from the north to the south (p. 19). Besides, there are daily, seasonal and annual fluctuations. To characterize the salinity conditions at a certain locality, the use of mean values are improper since, as can be seen in pp. 25 - 28, the variation is skew (unsymmetrical) and the rate of change is hidden. Tentatively the quartile values, quartile range and the frequency of changes describe the condition at a locality in a better way.

The general salinity situation in the area could be summed up in the following way (pp. 22, 29 - 30, Fig. 123). In the northern part (Kattegatt South) the salinity is relatively high, $q_2 = 18.27$ o/oo in the surface and 32.73 near the bottom at 25 m in depth. The quartile range, $q_3 - q_1$, varies from 5.50 o/oo at the surface and 6.87 at 15 m to 3.13 near the bottom. On the sill between Malmö and Copenhagen the surface values are low, $q_2 = 8.00$ o/oo and the quartile range 3.25. The figures from the bottom (8 m) are 9.22 o/oo and a quartile range of 9.73, the highest value found in the Öresund area. The frequency of changes is low, 0 - 20 (-28) % of the time, at 20 - 25 m in depth at Kattegatt South. At Oskarsgrundet, on the other hand, the frequency of variation at all depths varies from 0 to (65 -) 90 % of the time. The situation in the southernmost part (Falsterbo Reef) is much more stable with $q_2 = 6.69$ o/oo in the surface and 7.07 at the bottom and quartile ranges of 0.64 and 0.58 o/oo. The frequency of changes varies during January to September between 0 and 12 % of the time with an increase from September to December to about 30 %, due to the wind situation during autumn. Thus, the greatest quartile range and frequency of changes are found in the sill area.

The only parameter investigated which changes drastically from north to south and from the surface to the bottom in the area and shows the largest fluctuation is the salinity. Therefore, it can be assumed that the salinity may be one of the most important factors affecting the algal vegetation in the Öresund area.

Regional distribution

The number of benthic species which have been recorded along the Swedish coast is very suggestive. In Skagerack and the northern Kattegatt the number is about 350. In the northern part of the Öresund 214 and in the southern part 117 species have been found. In Blekinge about 110 marine species are known (Levring, 1940) and in the Öregrund archipelago about 70 (Waern, 1952). This means a reduction with 97 species within the Öresund, an area of 130 km's length.

The number of species within the three divisions in different parts of the Öresund compared with Bohuslän, mainly the Kristineberg area, and Blekinge is shown in Table 24. It is obvious that the percentage of brown algae diminishes rapidly from Bohuslän to the entrance of the Öresund. 51 % of the Swedish species have their southern border in the Kattegatt. The reduction of the number of red algae is 43 species in Kattegatt, amounting to 30 %. For the green algae 26 species (32 %) have their southern border in Kattegatt. When the situation within the Öresund is considered, it can be seen that 57 species of red algae have their

southern border in the Öresund and 28 species of brown algae. The decrease in the number of green algae is only 16 species. Thus, the reduction of red algae is further increased to 70 %, the largest part, 40 %, within the Öresund area. Corresponding values for the brown algae are 72 and 23 % and for the green algae 51 and 20 %. Certain species of brown algae evidently seem to be the first affected by decreasing salinity, whereas the red algae diminish at lower salinities as in the Öresund. As a consequence of the more pronounced reductions in the number of red and brown algal species, the percentage of green algae increases from 23 % in Bohuslän to 33 % in the southern Öresund. The number of species is further diminished in Blekinge. The figures for southern Öresund and Blekinge are, however, not quite comparable, partly because of the Baltic relict flora.

Table 24. Comparison of the composition of the algal flora in Bohuslän, the Öresund and Blekinge.

Area	Total number of species	Rhodophyta			Phaeophyta			Chlorophyta		
		n	% ¹	% ²	n	% ¹	% ²	n	% ¹	% ²
Bohuslän	346	142	100	41	124	100	36	80	100	23
N. Öresund	214	99	70	46	61	49	29	54	68	25
C. Öresund	156	72	49	45	40	32	26	44	55	29
S. Öresund	117	43 ^a	30	37	35 ^b	28	30	39 ^b	49	33
Blekinge	108	27 ^a	19	25	37 ^b	30	34	44 ^b	55	41

- 1 % of the number of species in the respective division in Bohuslän
- 2 % of the total number of species in the respective area
- a Ceramium tenuicorne only in S. Öresund and Blekinge
- b Sphacelaria plumigera, Dictyosiphon chordaria and Chaetomorpha linum in Bohuslän, S. Öresund and Blekinge

The number of species in Bohuslän is compiled from Kylin (1944, 1947, 1949) and Waern (1958) and in Blekinge from Levring (1940).

The main reason for the reduction in the number of species may primarily be correlated with the decreasing and fluctuating salinity. Another observation which supports the idea that the salinity factor is of major importance for the distribution of the algae, is the skew border lines from southwest to northeast which are found for e.g. Porphyra purpurea (p. 130), Petalonia fascia and Petalonia zosterifolia (p. 206), due to the somewhat higher salinity along the Danish coast, caused by the Coriolis effect. A similar phenomenon is the occurrence of belt-forming Porphyra linearis and Nemalion multifidum at the northern part of the island of Ven (p. 130), probably due to upwelling of more saline bottom water within this locality.

Concerning the regional distribution of the algae, it is noticeable that several of the pleioeuryhaline species, which are found more or less frequently in the Baltic and in the north part of the Öresund area, are found irregularly, or in some cases not at all, in the southern part of the Öresund (Limhamn - Skanör). These species are listed in Table 25.

Table 25. Species missing or less frequent in the area Limhamn - Skanör, compared with Blekinge and the north part of the Öresund area.

Missing species

RHODOPHYTA

Acrochaetium hallandicum
Audouinella efflorescens
Callithamnion furcellariae

PHAEOPHYTA

Entonema oligosporum
Myrionema magnussi

CHLOROPHYTA

Bolbocoleon piliferum

Less frequent species

RHODOPHYTA

Bangia fuscopurpurea
Acrochaetium parvulum
Rhodochorton purpureum
Ahnfeltia plicata
Polyides rotundus
Ceramium arborescens

PHAEOPHYTA

Spongonema tomentosum
Ralfsia verrucosa
Leptonematella fasciculata
Microspongium globosum
Leathesia difformis
Desmarestia viridis
Sphacelaria plumigera

CHLOROPHYTA

Chaetomorpha linum

The median values of salinity in the Limhamn - Skanör area are close to the values in the Baltic proper. Therefore, it is most probable that it is the large variation of the salinity in the area these species cannot withstand. The fluctuation index for the salinity (pp. 29 - 30) has here the highest value.

Experience from photosynthesis measurements has shown that sudden changes in the salinity of the medium cause severe disturbances in the photosynthesis (von Wachenfeldt, unpubl.). If these changes appear too often the disturbances will be too large, and sensitive algae cannot survive. Similar phenomena have been discussed by Gessner (1959) comparing the floral composition in the Baltic with some Norwegian fjords.

Vertical distribution

When the vertical distribution of the species in the Öresund area is compared with that of the corresponding species in Bohuslän and along the Norwegian coast, a change toward greater depths in the Öresund is found in many cases. This downward process is summarized in Fig. 124 A - E. About eight species of brown algae and four of green algae change their vertical distribution only a few metres downward and are not included in the list. As shown in the figure, the red algae are most affected. In the Öresund 43 species are found at greater depths than in Bohuslän. Among the brown algae 13 species have a changed vertical distribution and for the green algae only one species. This minor proportion of green algae might have been expected since they are mostly pleioeuryhaline and thus least affected by decreasing salinity. Besides, the composition of the pigments promotes the distribution of the green algae near the surface.

Trailliella intricata, *Corallina officinalis*, *Lithothamnion polymorphum* and *Plumaria elegans* are striking examples of the downward process among the red algae. They are in Bohuslän belt-forming from about 0.5 m below the 0-line and are found in the Öresund mainly from about 15 m in depth. The most prominent example among the brown algae is the behaviour of *Laminaria digitata* and *Laminaria saccharina*, which are both found belt-forming at 1 - 3 m in depth in Bohuslän and on the north side of Kullen, from 8 - 10 m on the southern side and not until 10 - 15 m in depth in the Öresund proper. A similar phenomenon can be studied in *Laminaria hyperborea*

which in the North Sea grows near the low-water mark in the tidal zone and is belt-forming in Skagerack and Kattegatt from 15 - 25 m in depth. *Fucus vesiculosus*, which in its entire distribution area grows in the littoral zone except in the Baltic, where it is always submerged, changes its vertical distribution to the sublittoral zone just south of Malmö.

A probable explanation of the downward process could be that diaspores from species, which are sensitive to decreasing salinity, are distributed within the whole water column but are only capable of germinating at such depths, where the salinity is high and stable enough. This is illustrated i.a. by the findings in the autumn at Kullen of numerous juvenile specimens of *Laurencia pinnatifida* at 10 m in depth. However, no mature specimens have ever been found in the Öresund area. The reduced pressure from competitors for space could also be a positive factor for colonization at greater depths, as the communities there are not so closed, this being especially notable on soft bottoms with pebbles and shells.

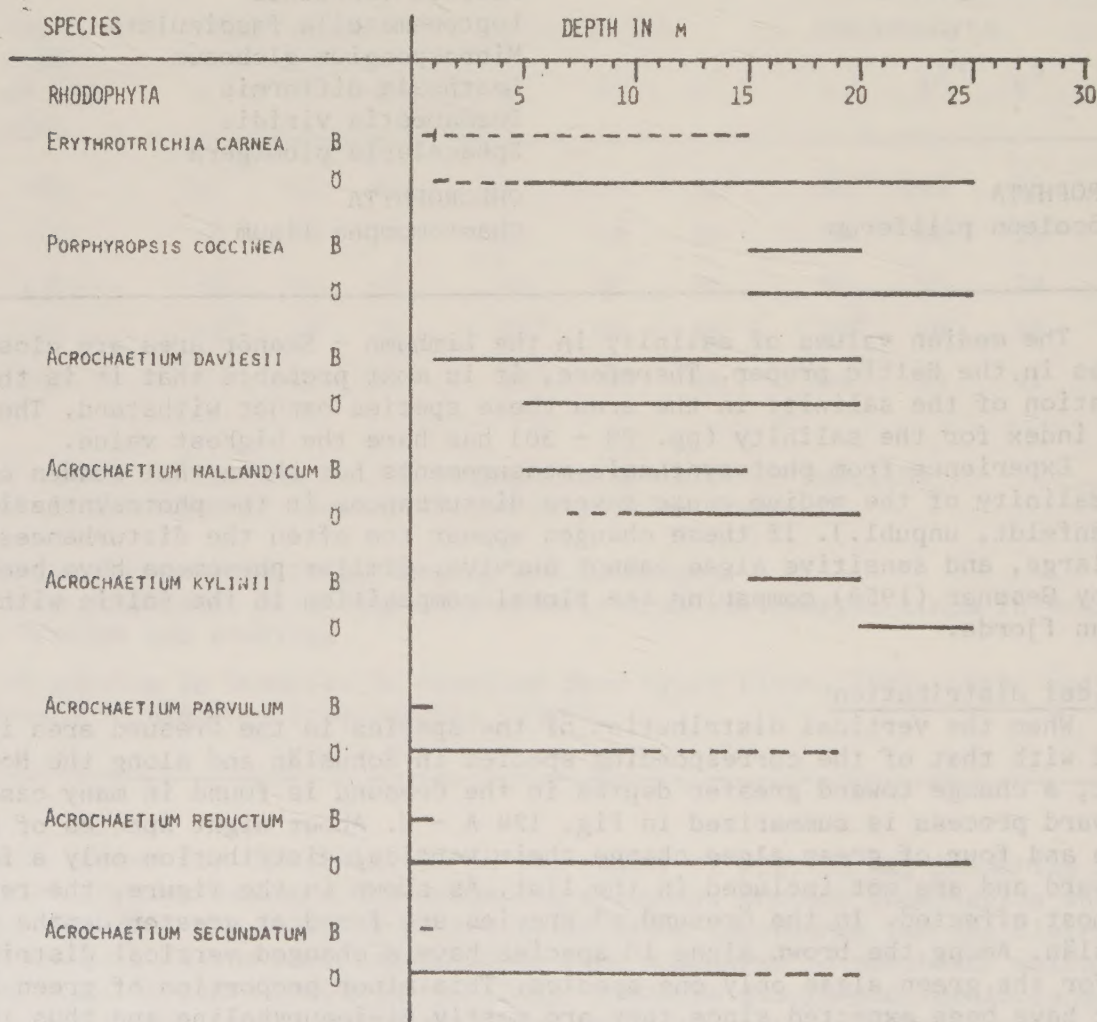


Fig. 124 A.

Fig. 124 A - E. Vertical distribution of algal species in the Öresund, compared with Bohuslän (Kylin, 1944, 1947, 1949).

B = Bohuslän — regularly found 1 = only at Kullen
 Ö = Öresund - - - occasionally found

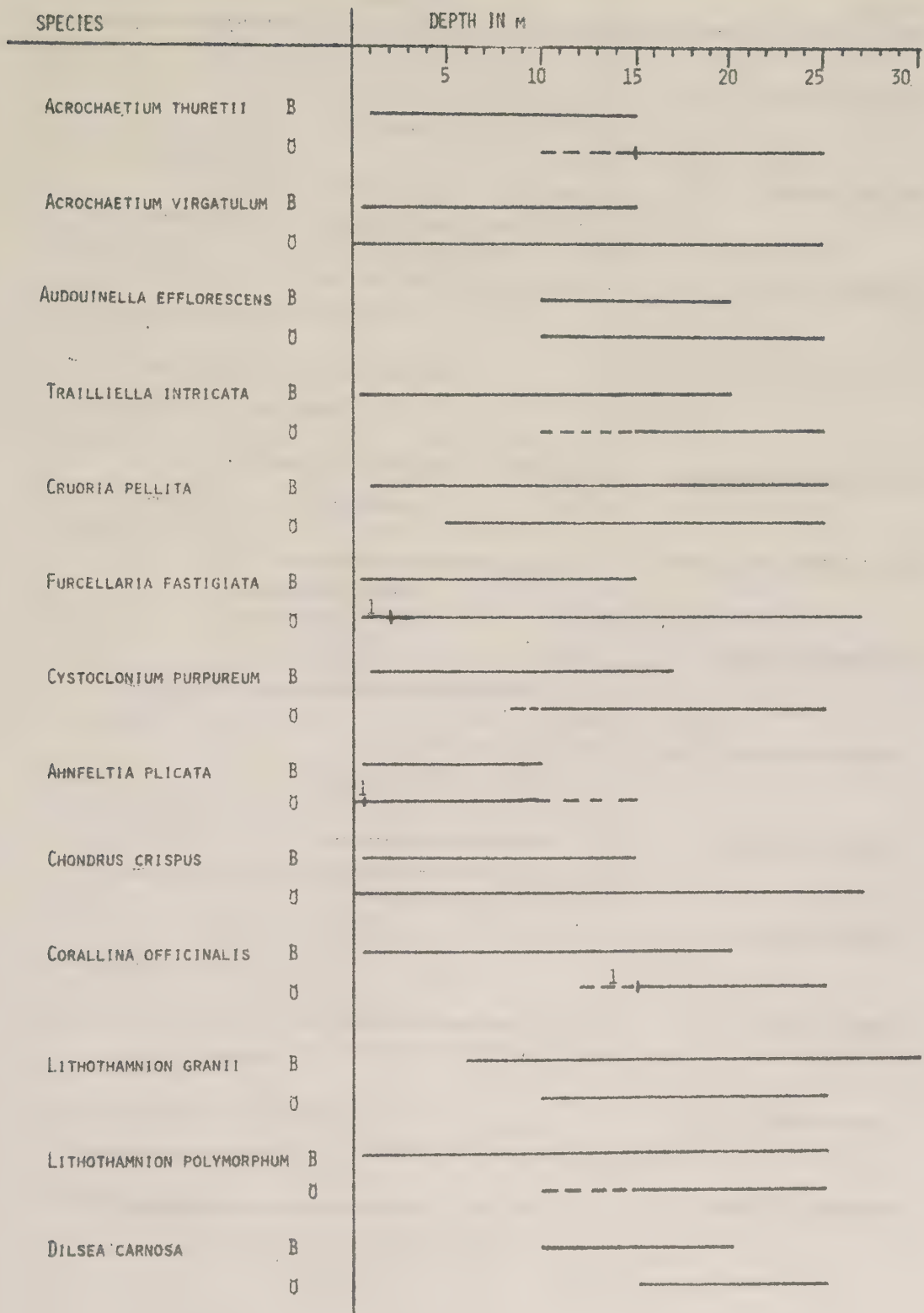


Fig. 124 B.

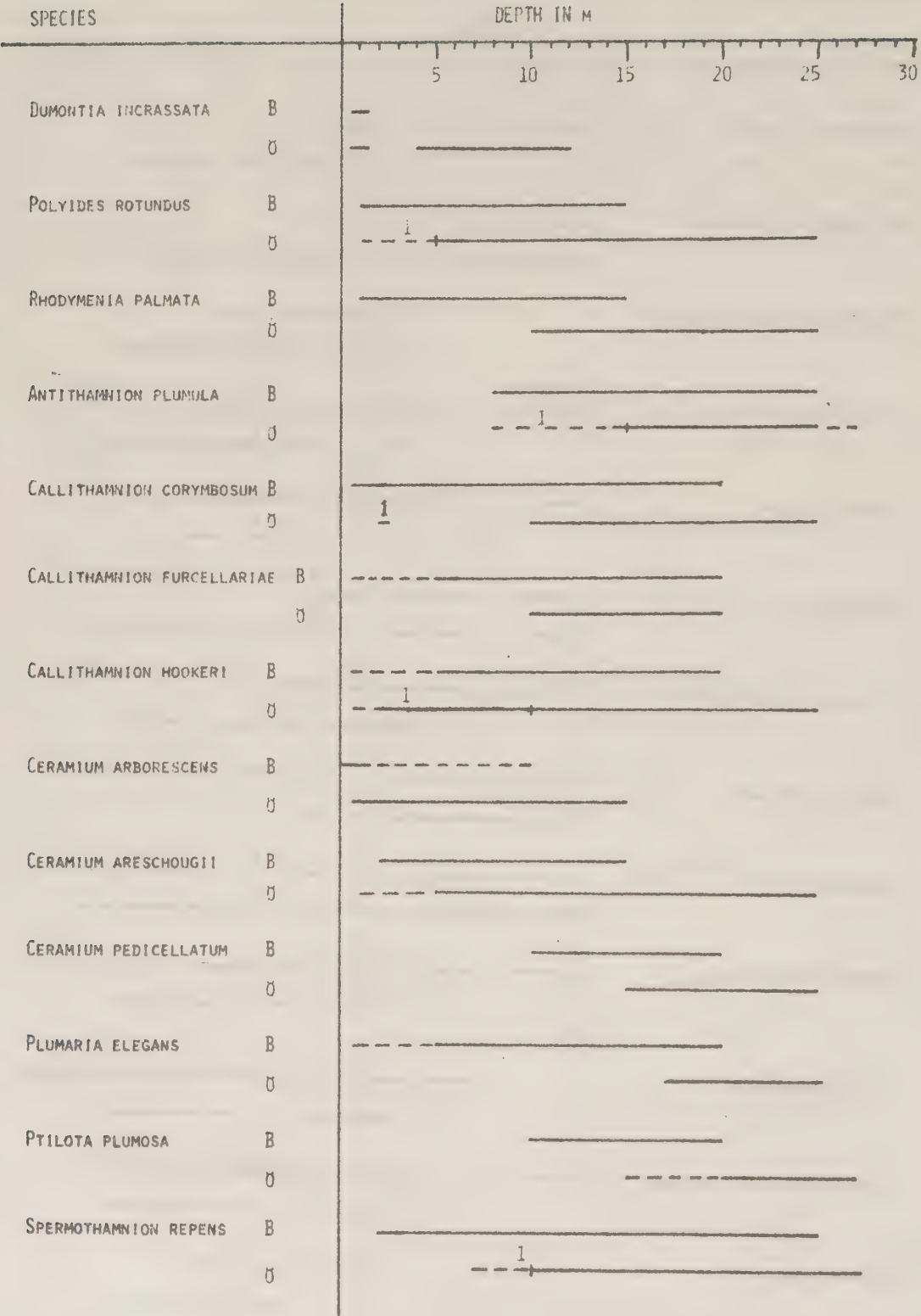


Fig. 124 C.

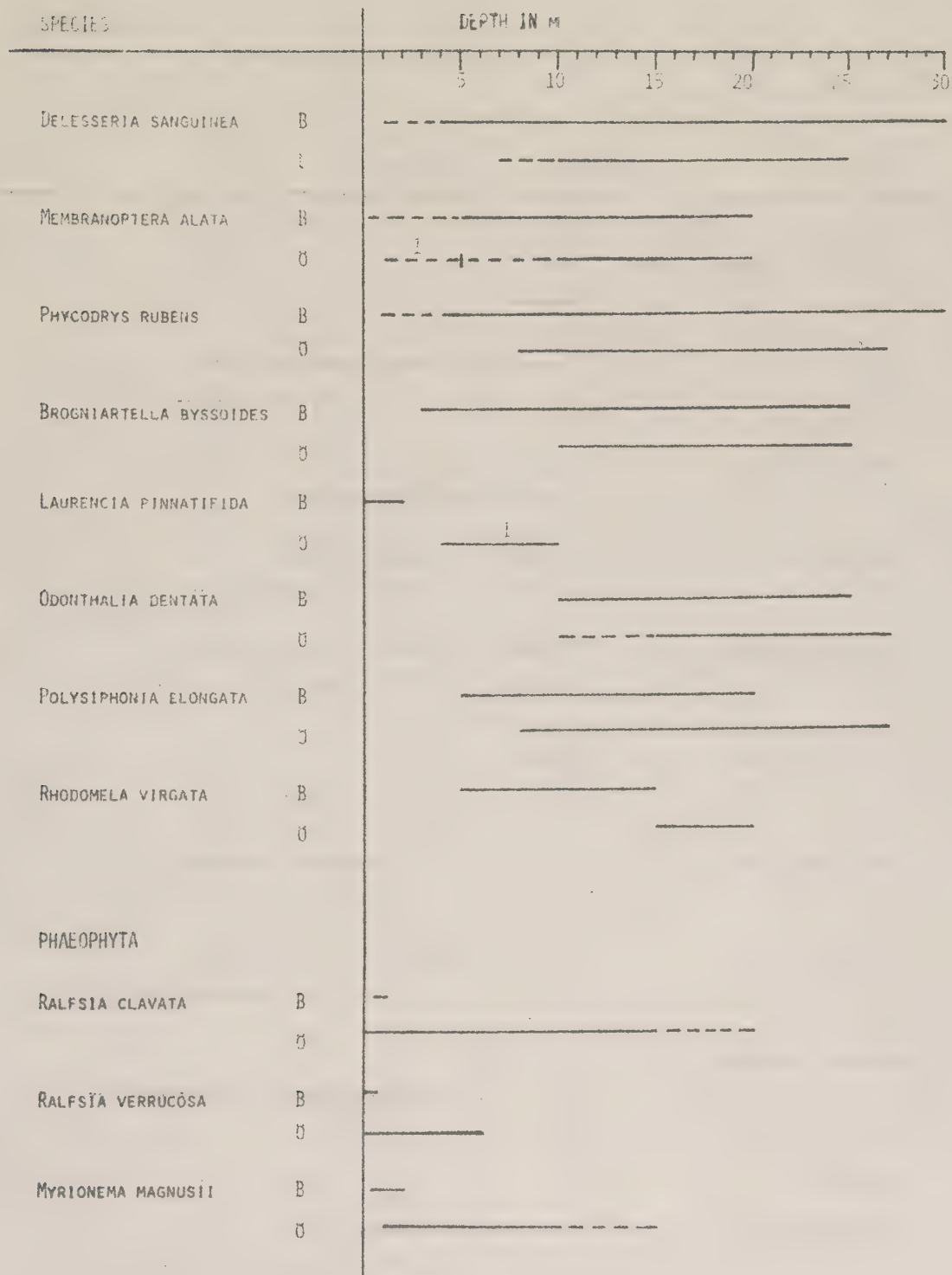


Fig. 124 D.

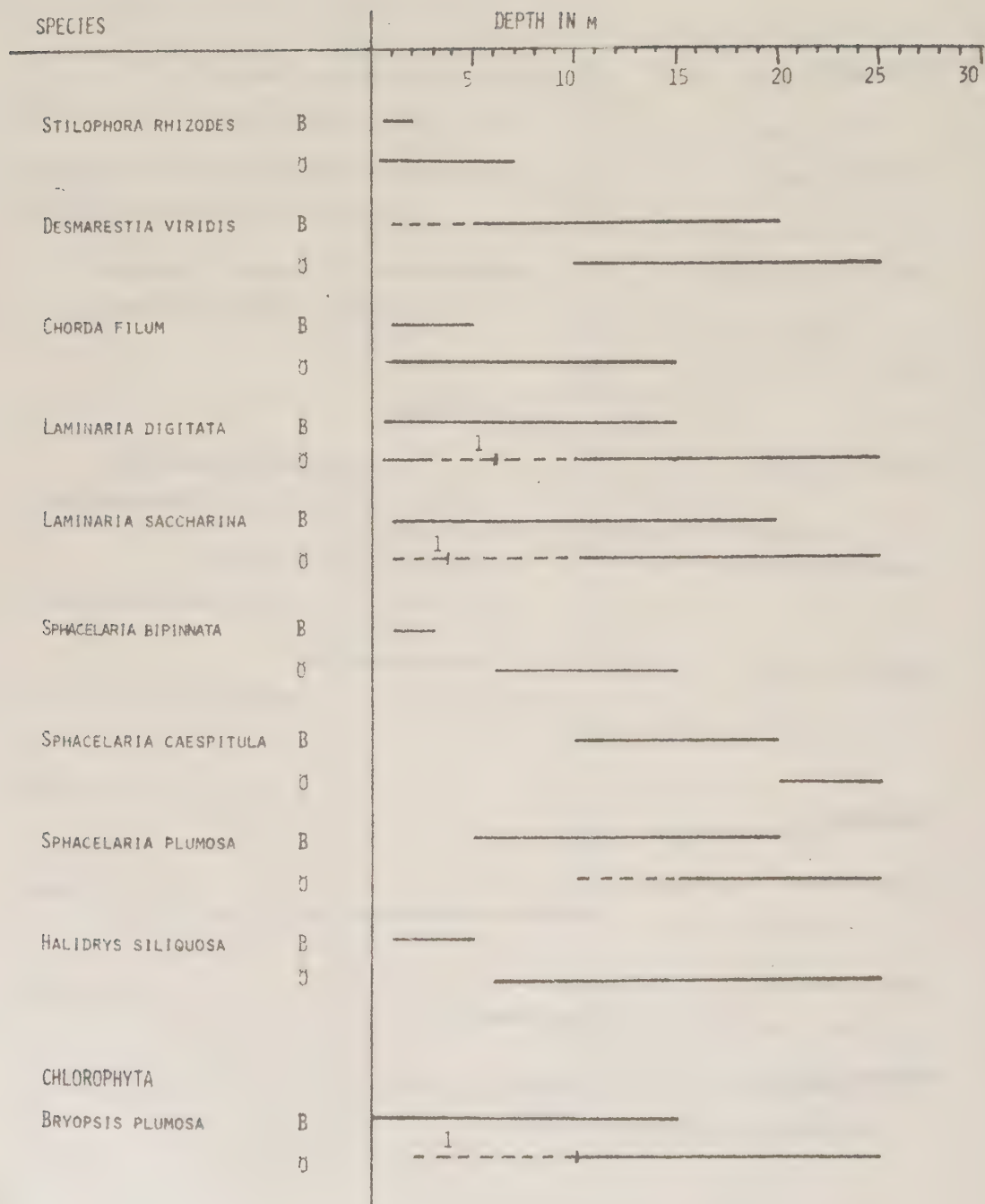


Fig. 124 E.

Morphology

It has been known for a long time that many species are reduced in size from north to south along the Swedish west coast and in the Baltic. This phenomenon has been discussed by i.a. Kylin (1907), Hylmö (1916), Levring (1940) and Waern (1952, 1965 a).

The figures for the actual size of different species and the variation with locality and depth of the investigation material from the Öresund have been given in section II. From these figures one can find a reduction either in the size of the cell or in the total size or in both. In Table 26 are shown the species which are reduced in comparison with their size in Bohuslän or are reduced within the Öresund area. For the calculation, the maximum length of the species has been used. Though, some extreme values of single observations, mainly from the northernmost part of the Öresund area, are omitted.

As can be seen in Table 26, 56 species (= 57 %) of the red algae found in N. Öresund are reduced in size in comparison with Bohuslän. The number of reduced brown algae is 18 equal to 30 %. Among the green algae only 5 species (= 9 %) are more or less reduced in size. There is in many cases a tendency to a further reduction from north to south in the Öresund area. A few species, which are reduced in size only within the Öresund area, are also added. Thus, the total number of reduced red algae is 60 species and for brown algae 20 species and green algae 6 species. The figures for the green algae are, however, somewhat uncertain, i.a. due to lack of reliable information about the size in Bohuslän. Besides, most green algae in the Öresund are as said above pleioeuryhaline and in some cases the species are larger than in Bohuslän probably due to eutrophication.

When evaluating the figures in Table 26 one has also to note that already in Bohuslän some species are somewhat reduced in comparison with the species in other areas, e.g. in the North Atlantic. Some examples are shown in Table 27.

That the decreasing and fluctuating salinity is the relevant factor for the morphological reduction can be illustrated by many examples. In the north part of the Öresund there is a marked difference in the total size of e.g. *Furcellaria fastigiata*, *Ptilota plumosa*, *Delesseria sanguinea*, *Phycodrys rubens* and *Rhomela confervoides* above and below the halocline with larger specimens at greater depths (Table 26). *Corallina officinalis* and *Spermothamnion repens* behave in the same way. On the other hand, south of the threshold between Malmö and Copenhagen only dwarf forms of certain species, e.g. *Delesseria sanguinea*, *Membranoptera alata* and *Phycodrys rubens*, are to be found. These phenomena are exemplified in Fig. 125. The substratum is similar in the whole area. In areas A and C the light and temperature conditions are also similar. If the poorer light conditions because of the greater depth in area B had any effect on the morphology of the species, these specimens would be more reduced. The only parameter that may induce a higher growth is thus the salinity.

The morphology of some species is also affected by temporarily increased salinity due to high winds from northwest, of either greater strength or longer duration than normal. The following examples can be taken. In 1967 during October and the beginning of November similar conditions were found in the Öresund. The period coincided with the germination of *Porphyra linearis* at the island of Ven in the middle of the Sound. *Porphyra linearis* at this locality has normally extremely reduced thalli, 1 - 2 mm broad and about 30 mm long, but in November 1967 the thalli were 8 - 10 (- 12) mm broad and 18 - 20 (- 23) cm long. Furthermore, the specimens were much more numerous than usual.

Sometimes the fluctuating salinity rather than the decreasing salinity may play a role as a growth inhibitor. *Callithamnion furcellariae* seems to be sensitive to fluctuating salinity but apparently not to low salinity. In the Öresund the species reaches a length of 1.5 - 2.5 (- 3) cm; in the Baltic, however, e.g. at Bornholm and in Blekinge, it will grow at corresponding depths to a length of (3 -) 4 - 5 (- 8) cm (Levring, 1940).

Besides the direct changes in morphology, viz. the total and cell size, other changes have been observed in some cases. In *Trailliella intricata* there is besides the reduction from 3 to about 0.5 cm in length also a noticeable reduction in the number of glandular cells. In the case of *Fucus distichus* ssp.

edentatus the number of caeostomata is reduced from about 500/cm² to 10 - 20/cm².

In some cases changes in morphology may be due to other factors than salinity, e.g. reduced light intensity in combination with shorter vegetation period. Halidrys siliquosa, which in Bohuslän and Halland is found only between 1 and 5 m in depth, shows normal growth and development in the north part of the Öresund from 6 - 15 m in depth but is reduced in size and sterile from 15 - 25 m in depth. If the vertical distribution is changed from the upper part of the sublittoral zone to the lowermost part of the same zone near the compensation depth, this will result in reduced size. This is also one possible explanation of the findings of reduced specimens of Ahnfeltia plicata from 10 - 15 m in depth and of extremely reduced Callithamnion hookeri at 25 m in depth near the island of Ven.

Table 26. The length in cm of different species in Bohuslän, N. Öresund and S. Öresund and the degree of reduction in % of the size in Bohuslän (Kylin, 1944, 1947, 1949).

B = Bohuslän 1 = above the halocline
NÖ = N. Öresund 2 = below the halocline
SÖ = S. Öresund or the south border of the species

Species	Length in cm			Degree of reduction	
	B	NÖ	SÖ	B-NÖ in %	B-SÖ
RHODOPHYTA					
Goniotrichum alsidii	0.5	0.3	0.3	40	40
Erythrocladia irregularis	0.006	0.004	-	35	-
Erythrotrichia carnea	3	1	1	65	65
Porphyropsis coccinea	1	0.4	0.4	60	60
Bangia fuscopurpurea	10	6	6	40	40
Porphyra linearis	25	12	3	50	90
Porphyra purpurea	20	15	15	25	25
Porphyra umbilicalis	20	10	10	50	50
Acrochaetium collopodum	0.02	0.015	0.015	25	25
Acrochaetium daviesii	0.2	0.1	-	50	-
Acrochaetium hallandicum	0.1	0.07	0.07	30	30
Acrochaetium leptonema	0.03	0.025	0.025	15	15
Acrochaetium parvulum	0.035	0.02	0.02	45	45
Acrochaetium pectinatum	0.3	0.2	-	35	-
Acrochaetium secundatum	0.15	0.1	0.1	35	35
Acrochaetium thuretii	0.3	0.2	-	35	-
Acrochaetium virgatulum	0.3	0.2	0.2	35	35
Audouinella efflorescens	0.4	0.2	0.2	50	50
Rhodochorton penicilliforme	0.4	0.15	0.15	60	60
Rhodochorton purpureum	0.5	0.3	0.3	40	40
Nemalion multifidum	20	12	4	40	80
Trailliella intricata	3	0.4	0.4	85	85
Cruoria pellita	15	15	2	0	85
Furcellaria fastigiata 1	10	6	-	40	-
Furcellaria fastigiata 2	20	20	12	0	40
Cystoclonium purpureum	30	20	10	35	65
Ahnfeltia plicata	15	10	5	35	65
Ceratocolax hartzii	0.4	0.3	0.3	25	25
Phyllophora membranifolia	15	12	7.5	20	50
Chondrus crispus	15	12	5	20	65
Rhodophysema elegans	0.3	0.15	-	50	-
Corallina officinalis	6	5	2	15	65

Table 26 (continued).

Species	Length in cm			Degree of reduction in %	
	B	NÖ	SÖ	B-NÖ	B-SÖ
<i>Lithothamnion granii</i>	1.5	0.3	0.1	80	95
<i>Lithothamnion lenormandii</i>	20	20	3	0	85
<i>Dumontia incrassata</i>	40	22	12	45	70
<i>Polyides rotundus</i>	15	10	5	35	65
<i>Harveyella mirabilis</i>	0.2	0.1	0.05	50	75
<i>Rhodymenia palmata</i>	30	20	10	35	65
<i>Antithamnion plumula</i>	8	3	0.5	60	95
<i>Callithamnion corymbosum</i>	6	2	0.5	65	90
<i>Callithamnion hookeri</i>	3	4	0.3	0	90
<i>Callithamnion tetragonum</i>	7	6	3	15	55
<i>Ceramium arborescens</i>	15	12	12	20	20
<i>Ceramium areschougii</i>	25	15	-	40	-
<i>Ceramium pedicellatum</i>	15	12	-	20	-
<i>Ceramium strictum</i> s.l.	8	5	3	35	60
<i>Plumaria elegans</i>	8	2	-	75	-
<i>Ptilota plumosa</i> 1	12	3	-	75	-
<i>Ptilota plumosa</i> 2	12	12	3	0	75
<i>Spermothamnion repens</i>	4	0.7	0.2	80	95
<i>Delesseria sanguinea</i> 1	25	8	5	70	80
<i>Delesseria sanguinea</i> 2	25	20	-	20	-
<i>Membranoptera alata</i>	12	10	2	15	85
<i>Phycodrys rubens</i> 1	10	3	2	70	80
<i>Phycodrys rubens</i> 2	10	8	-	20	-
<i>Brogniartella byssoides</i>	20	16	2	20	90
<i>Odonthalia dentata</i>	20	15	12	25	40
<i>Polysiphonia brodiaei</i>	15	7	-	55	-
<i>Polysiphonia elongata</i>	25	25	10	0	60
<i>Polysiphonia fibrillosa</i>	20	15	-	25	-
<i>Polysiphonia nigrescens</i>	25	20	15	20	40
<i>Polysiphonia urceolata</i>	10	6	5	40	50
<i>Rhodomela confervoides</i> 1	20	10	10	50	50
<i>Rhodomela confervoides</i> 2	20	15	-	25	-
<i>Rhodomela virgata</i>	30	15	-	50	-
PHAEOPHYTA					
<i>Spongonema tomentosum</i>	10	6	4	40	60
<i>Ralfsia verrucosa</i>	10	10	3	0	70
<i>Hecatonema diffusum</i>	0.025	0.01	0.01	60	60
<i>Leptonematella fasciculata</i>	0.3	0.2	0.2	35	35
<i>Microspongium globosum</i>	0.2	0.1	-	50	-
<i>Myrionema coronnae</i>	0.2	0.1	-	50	-
<i>Leathesia difformis</i>	5	0.7	0.7	85	85
<i>Chordaria flagelliformis</i>	50	30	25	40	50
<i>Eudesme virescens</i>	15	12	12	20	20
<i>Stilophora rhizodes</i>	20	10	-	50	-
<i>Myriotrichia clavaeformis</i>	15	12	-	20	-
<i>Desmotrichum undulatum</i>	15	5	5	65	65
<i>Petalonia fascia</i>	15	15	10	0	35
<i>Petalonia zosterifolia</i>	?	12	8	?	(35)
<i>Desmarestia aculeata</i>	100	60	60	40	40
<i>Laminaria saccharina</i>	?	150	50	?	(65)
<i>Sphacelaria bipinnata</i>	3	2	-	35	-
<i>Sphacelaria cirrosa</i>	1.5	1	1	35	35
<i>Sphacelaria plumosa</i>	10	5	3	50	70

Table 26 (continued).

Species	Length in cm			Degree of reduction in %	
	B	NÖ	SÖ	B-NÖ	B-SÖ
<i>Fucus distichus</i> ssp <i>edentatus</i>	30	25	15	15	50
<i>Fucus spiralis</i>	25	10	-	60	-
<i>Halidrys siliquosa</i> 1	100	90	-	10	-
<i>Halidrys siliquosa</i> 2	100	25	-	75	-
CHLOROPHYTA					
<i>Enteromorpha ahlneriana</i>	40	30	30	25	25
<i>Chaetomorpha aerea</i>	30	5	-	85	-
<i>Chaetomorpha melagonium</i>	30	15	15	50	50
<i>Cladophora rupestris</i>	20	12	12	40	40
<i>Urospora wormskioldii</i>	20	12	12	40	40
<i>Bryopsis plumosa</i>	12	15	5	0	65

Table 27. The maximum length in cm of some species in the North Atlantic, Bohuslän and the Öresund.

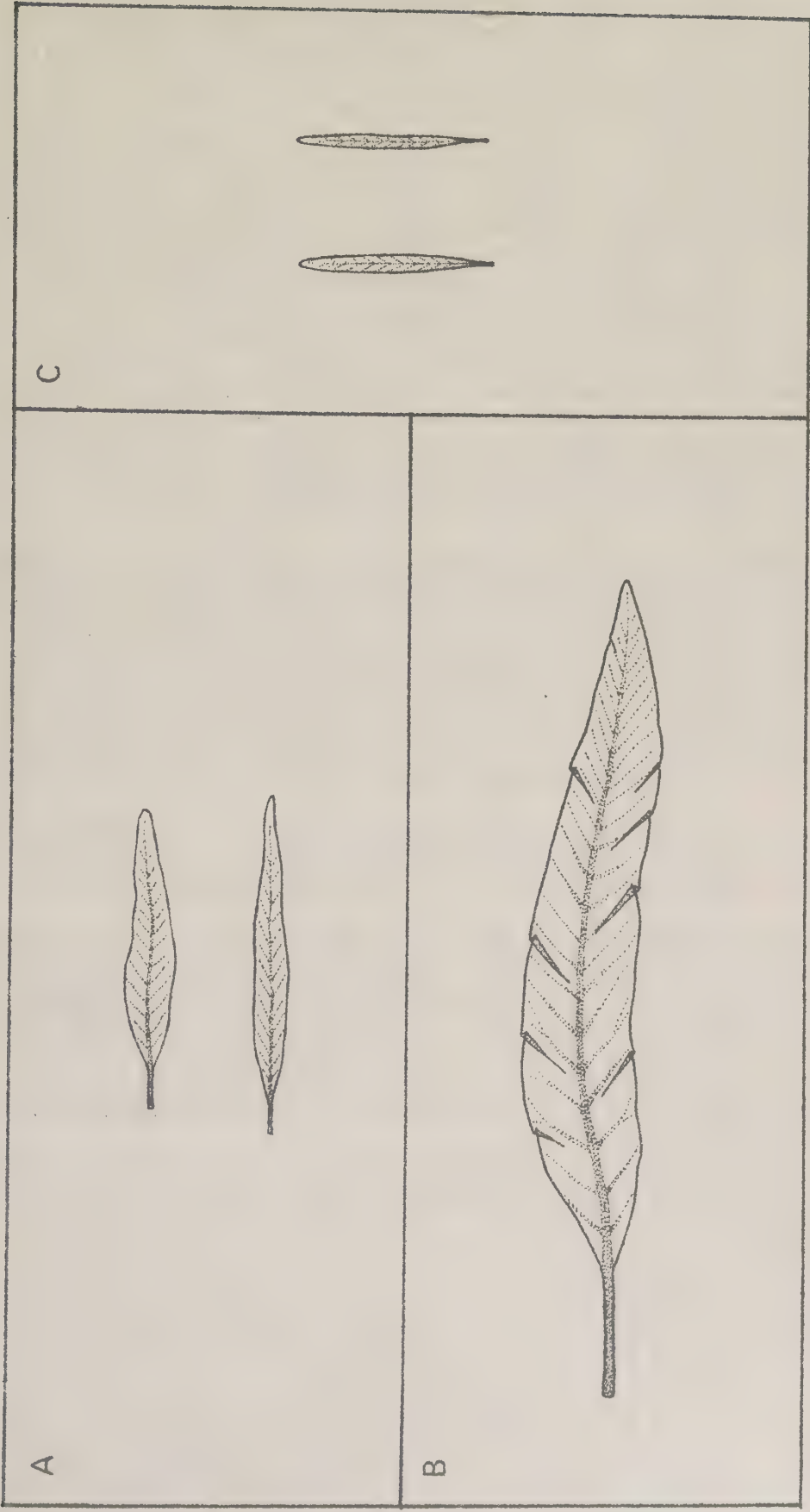
Species	North Atlantic	Bohuslän ⁴	N.Öresund
<i>Rhodymenia palmata</i>	100 ¹	30	20
<i>Antithamnion plumula</i>	12 ²	8	3
<i>Plumaria elegans</i>	20 ²	8	2
<i>Delesseria sanguinea</i>	30 ³	25	8
<i>Odonthalia dentata</i>	30 ²	20	15

1 Rex (1970)

2 Taylor (1937)

3 own observation from Helgoland

4 Kylin (1944)



5cm

Fig. 125. Variation in morphology of *Delesseria sanguinea*.

A = in the north part of the Öresund, above the halocline
B = in the north part of the Öresund, below the halocline
C = in the south part of the Öresund

Reproduction

Especially among the red algae in the Öresund area, there is a tendency to a loss of sexual reproduction when the environmental factors become poorer. If the conditions deteriorate further it may result in a loss of the ability to asexual reproduction and the species become sterile at the fringe of their distribution area. These species are listed in Fig. 126.

Concerning the red algae, Dixon (1965) writes "in the centre of distribution of each species there are both haploid and diploid plants, with the majority of each type being fertile and producing sexual organs, and thence carposporangia or tetrasporangia respectively, with a few plants of each type remaining sterile. In the penultimate zone, the conditions are such that the expression of sexual potential is inhibited; here, the haploid plants are entirely sterile with some of the diploid plants producing tetrasporangia. Finally, at the northern limits of distribution the reproductive potential of both haploid and diploid plants is incapable of expression so that all plants are sterile". Dixon discusses these matters by comparing the algal vegetation at the Spanish Atlantic coast and the coast of Great Britain. Unfortunately, he does not give information as to which one of the factors affects the algae in the described manner. The salinity factor can be omitted in his example as the difference in salinity between the two areas is negligible. Apparently a change in one or more environmental factors may give the same result.

Dixon's statement can easily be adopted to the conditions in the Öresund and the Baltic. The limits for the different reactions must of course vary from species to species and for a certain species even from year to year depending on the actual salinity condition. For some species, e.g. *Antithamnion plumula*, *Callithamnion corymbosum*, *Callithamnion tetragonum* and *Ptilota plumosa*, the limit for sexual reproduction is found in the area Kullen - Grållegrund and for asexual reproduction between Grållegrund and Landskrona (Fig. 126). The southern border for *Porphyra purpurea* and *Porphyra umbilicalis* is found between Landskrona and Copenhagen (Dragör) but the conchocelis stage is common further south down to the line Dragör - Skanör.

Some species are also spread by means of monospores or paraspores but even this way of propagation may be disturbed in extreme conditions. This is the case for e.g. *Asterocytis ramosa*, *Porphyropsis coccinea*, *Callithamnion hookeri* and *Plumaria elegans*.

The disturbances of reproduction seem to be predominant among the red algae. Hardly any such observations have been made among the brown algae, but in a few cases among the green algae. Thus, *Spongomorpha aeruginosa*, *Urospora penicilliformis* and *Urospora wormskioldii* normally have a heteromorphic life-cycle. This does not seem to be the case in the Öresund, where the *Chlorochytrium* and *Codiolum* stages are absent or rare. The reason is not yet clarified although the reduced salinity may be the trigger factor. On the other hand, *Derbesia marina* lacks its *Halicystis* stage in the Öresund area.

To maintain the population in areas where the algae are not capable of sexual reproduction there must be an inflow of diaspores (carpospores or tetraspores). This may be the case for e.g. *Antithamnion plumula*, *Callithamnion corymbosum*, *Ptilota plumosa*, *Laurencia pinnatifida*, *Polysiphonia brodiaei* and *Derbesia marina*. For species, such as *Polysiphonia nigrescens* and *Rhodomela confervoides*, which have decreased ability to sexual reproduction in the southern Öresund and are almost completely sterile in the Baltic (Levring, 1940), the explanation is not so easy. In the southern Öresund an inflow of carpospores or tetraspores from the northern part might be possible but a propagation from the northern Öresund and the Belt Sounds even into the Baltic seems less probable. To explain the latter, two theories may be offered. Firstly, the meiosis at the tetraspore formation could be disturbed or even lacking, resulting in only diploid specimens. An interesting question is then also where and at which salinity this would occur. Secondly, the algae could be spread vegetatively and survive unfavourable periods by means of a few cells. The latter seems less probable, though it is known to be the case for certain brown algae, e.g. *Sphacelaria plumigera* and *Halopteris scoparia*.

	Bohuslän	Halland	HV	Ku	Hö	Gr	He	La	Ba	Lo	Ma	Kl	Bt	Fa
<i>Asterocytis ramosa</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx
<i>Porphyropsis coccinea</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx
<i>Acrochaetium hallandicum</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx
<i>Acrochaetium thuretii</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx	xxxxxx
<i>Audouinella efflorescens</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Cruoria pellita</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Petrocelis hennedyi</i>	+++++	?	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Ceratocolax hartzi</i>	+++++	?	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Corallina officinalis</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Dilsea carnosa</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Anthamnia boreale</i>	+++++	?	000000	000000	000000	000000	000000	000000	000000	000000	000000	000000	000000	000000
<i>Anthamnia plumula</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Callithamnion corymbosum</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Callithamnion hookeri</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Callithamnion tetragonum</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Ceramium arborescens</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Ceramium pedicellatum</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Filumaria elegans</i>	+++++	?	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Ptilota plumosa</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Spermothamnion repens</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Phycodrys rubens</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Broggiartella byssoides</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Cdonthalia dentata</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Polysiphonia elongata</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Polysiphonia nigrescens</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Polysiphonia urceolata</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++
<i>Rhodomela confervoides</i>	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++	+++++

Fig. 126. Species of red algae with reduced ability to sexual or asexual reproduction in the Öresund area. The material from Bohuslän and Halland compiled from Kylin (1944).

specimens with sexual organs	HV = Hallands Väderö	Ba = Barsebäck
specimens with decrease in number of sexual organs	Ku = Kullen	Lo = Lomma Bay
specimens with tetraspores	Hö = Höganäs	Ma = Malmö
specimens with monospores	Gr = Grållegrund	Kl = Klagshamn
sterile specimens	He = Helsingborg	Br = Bredgrund
	La = Landskrona	Fa = Falsterbo

Different kinds of south borders

As said above the number of species is strongly reduced from the north to the south in the Öresund with 97 species over a distance of only 130 km. A closer examination of those algae which have their southern border in the Öresund reveals that different species react in different ways near their distribution border.

Four groups of species with different kinds of south border may be distinguished:

1. Species with a definitely marked south border which is surprisingly constant for a long period. These species do not decrease in abundance or change their morphology, fructification or vertical distribution. To this group belongs only *Ascophyllum nodosum*. The south border for this species has been constant at Mölle, at least since the later part of the 19th century (cf. Simmons, 1898). The species is belt-forming, fertile and of normal size. Despite the flow of gametes or zygotes from the north, the species has not been able to penetrate further into the Sound, although suitable substratum is found at many localities. An interesting question is if the fungus *Mycosphaerella ascophylli* Cotton, which is allied with *Ascophyllum nodosum* according to Kohlmeyer (1972), plays any role for the distribution pattern. It is also noticeable that there are no finds of *Ascophyllum nodosum* on the Danish side of the Sound.

2. Species with a relatively marked south border which does not fluctuate. These species have a decreasing abundance, little or moderate change in morphology and no change in fructification or vertical distribution. To this group belong *Porphyra purpurea*, *Porphyra umbilicalis*, *Chordaria flagelliformis*, *Petalonia fascia*, *Petalonia zosterifolia*, *Desmarestia aculeata*, *Fucus distichus* ssp. *edentatus* and *Fucus spiralis*. *Fucus spiralis* is belt-forming in the normal way at Hallands Väderö and Hovs Hallar. South of this line the species is less frequently found and somewhat reduced in size but without change in fructification and vertical distribution.

3. Species with a diffuse but not fluctuating south border. These species gradually decrease in abundance, change morphology and reduce their fertility. They also change the vertical distribution to greater depth. This group includes *Cruoria pellita*, *Cystoclonium purpureum*, *Corallina officinalis*, *Epilithon membranaceum*, *Lithothamnion granii*, *Lithothamnion lenormandii*, *Lithothamnion polymorphum*, *Dilsea carnosa*, *Rhodymenia palmata*, *Callithamnion tetragonum*, *Ptilota plumosa*, *Spermothamnion repens*, *Odonthalia dentata*, *Laminaria digitata*, *Laminaria saccharina*, *Halidrys siliquosa* and *Bryopsis plumosa*. Several of these species are found in the littoral zone and the first metres of the sublittoral zone in Bohuslän. In the Öresund they are as a rule found below the halocline. Near the south border one finds only a few specimens which often are reduced.

4. Species with a relatively marked but oscillating south border. These species show decreasing abundance, changes in their morphology, reduced ability to reproduce and compete for space, and in some cases also change their vertical distribution. Some of the species are only found in the north part of the area in low numbers and not every year. These species are *Euthora cristata*, *Callithamnion bipinnatum*, *Ceramium penicillatum*, *Laurencia pinnatifida*, *Polysiphonia brodiaei*, *Microsyphar porphyrae*, *Sorocarpus ovaeformis*, *Litosiphon pusillus*, *Punctaria plantaginea*, *Prasinocladus lubricus*, *Pilinia rimosa* and *Derbesia marina*. Other species are frequently found in the north part of the area but their southern border oscillates. This group includes *Porphyropsis coccinea*, *Porphyra linearis*, *Nemalion multifidum*, *Antithamnion plumula*, *Callithamnion corymbosum*, *Callithamnion hookeri*, *Ceramium areschougii*, *Plumaria elegans*, *Broggiartella byssoides*, *Polysiphonia fibrillosa*, *Microspongium gelatinosum*, *Sphacelaria bipinnata*, *Sphacelaria plumosa* and *Chaetomorpha aerea*. The southernmost colonization may depend on a higher salinity than normal during the time for germination and that a suitable substratum is free from competitors.

Ecological demands

As has been shown, many species are adapted to the unstable salinity conditions by means of changes in morphology and vertical distribution and in reduced ability to reproduce. In some cases one can also find a sudden change in the eco-

logical demand of the species. *Porphyra linearis* and *Nemalion multifidum* are both common and belt-forming on exposed localities along the coast of Bohuslän, Halland and in the north part of the Öresund south to Mölle. South of this locality one can find single reduced specimens but only at very sheltered localities, except on the northern part of the island of Ven, where the two species show a nearly normal appearance probably due to upwelling saline water. The same tendency is shown by Lewis (1968) who is of the opinion that *Fucus vesiculosus* near its northern distribution limit becomes less tolerant of exposure. This may also be the explanation of the sudden change in vertical distribution for *Fucus vesiculosus*, which has been demonstrated on p. 224. It has sometimes been assumed that this behaviour of *Fucus vesiculosus* in the Baltic should be an effect of ice-scraping in the littoral zone. This is not a possible explanation for the conditions in the south part of the Öresund, where ice-scraping is hardly ever found.

In the sublittoral zone species like *Corallina officinalis*, *Dilsea carnosa* and *Odonthalia dentata* cannot compete successfully with other species in the normal communities and consequently are found in very limited numbers. On soft bottoms with old shells and pebbles, however, these species can survive and even become common, because there are no closed algal communities on such bottoms. Waern (1958), who reaches the same conclusion concerning the shell bottoms in Bohuslän, maintains that "the shell-bottoms are our reservations for weakly competitive individuals of species, living on the fringes of their distribution range".

Delay in development

If the vegetation period for species in the Baltic is compared with that in Skagerack and Kattegatt, one can for certain species find a trend towards a delayed or in some cases much delayed development in the Baltic (cf. Levring, 1940). This is the case for e.g. *Eudesme virescens*, *Scytosiphon lomentaria*, *Ulothrix-Urospora* sp. and *Cladophora glomerata*. Kylin (1907) was of the opinion that the algal flora in the southern part of Halland developed later than in Bohuslän, and referred to e.g. *Dumontia incrassata*, *Harveyella mirabilis*, *Ptilota plumosa*, *Dellesseria sanguinea* and *Rhodomela confervoides*. According to the author's opinion these species do not develop later in the Öresund than in Bohuslän. At 4 - 12 m in depth *Dumontia incrassata* is found in good condition in July but in this case it is probably not the salinity but more likely the light and temperature conditions which make the species survive longer. Whether the flora really does develop later along the coast of Halland and the Öresund compared with Bohuslän is hard to say but it seems not to be the truth. The observations made by Kylin (loc. cit.) could be within the range of the natural variation of the development during different years.

The time for the occurrence of *Nemalion multifidum* in the central and south part of the Öresund is not considered as an example of delayed development. At Hallands Väderö and Kullen the species appears at the same time as in Bohuslän, in the later part of July, and is fully developed in August and September. In the central and south part (except the northern part of the island of Ven) single specimens are found in late September and are fully developed in October and November. This coincides well with the higher salinities found in these areas in the autumn.

The actual border for the delayed development of the algal flora is not to be found in Kattegatt or the Öresund but in the entrance to the Baltic. The reason for this is probably not the salinity but the temperature factor. When the fructification periods for different species in Bohuslän and the Öresund are compared, no delay in development can be found.

Short-term variation in the floral composition

Within an area where the salinity varies not only from day to day but from month to month and even during longer periods, the composition of the algal vegetation must fluctuate. A species is able to grow in an area where it can survive the extreme values and is adapted to the daily fluctuation. Some species are probably more sensitive to salinity changes during certain periods of their development than during others, e.g. in juvenile stages, Nygren (1966). Small changes in

salinity are of course most noticeable for the annuals but to some extent also for perennial algae. Such fluctuations in the algal communities are very difficult to record with currently used methods. One has to know the composition of the flora at different stations in detail. This is possible in the littoral zone but very difficult in the sublittoral. During this investigation some localities have been followed in detail for many years, which has made it possible to follow the fluctuations of the flora. Such localities are the littoral zone and the upper part of the sublittoral zone at Hallands Väderö, Kullen, Barsebäck and Klagshamn and the deeper part of the sublittoral zone at Kullen and Grällegrund. The noted fluctuations in the qualitative and quantitative composition of the vegetation may depend on many factors i.e. changes in water level, degree of exposure, temperature and salinity. In Table 28 are listed the species, which may occur in larger frequency in connexion with higher salinity.

Table 28. Species with fluctuating abundance from year to year.

RHODOPHYTA		
Porphyropsis coccinea	Callithamnion corymbosum	Litosiphon pusillus
Porphyra linearis	Callithamnion hookeri	Punctaria plantaginea
Acrochaetium dumontiae	Ceramium penicillatum	Petalonia zosterifolia
Acrochaetium emergens	Plumaria elegans	Sphacelaria bipinnata
Acrochaetium macula	Ptilota plumosa	Sphacelaria plumosa
Acrochaetium moniliforme	Spermothamnion repens	Fucus spiralis
Nemalion multifidum	Laurencia pinnatifida	
Ceratocolax hartzii	Polysiphonia brodiaei	CHLOROPHYTA
Polyides rotundus	Polysiphonia fibrillosa	Prasinocladus lubricus
Euthora cristata		Pilinia rimosa
Antithamnion plumula	PHAEOPHYTA	Chaetomorpha aerea
Callithamnion bipinnatum	Microsyphar porphyrae	Bryopsis plumosa
	Sorocarpus uvaeformis	

Long-term variation in the floral composition

The long-term variation in salinity has been described on p. 21. High values of salinity occurred in 1950-52, 1959-61 and 1968-69. The increased salinity has resulted in a colonization by several animal species in the Öresund according to i.a. Nordenberg (1962). For the algal flora it has not been possible to prove any such effect. However, some species, e.g. Trailliella intricata, Spermothamnion repens, Polysiphonia brodiaei, Polysiphonia fibrillosa and Chaetomorpha aerea, may possibly have increased temporarily in number during the late sixties. It is likely that although the salinity mean values have increased, the frequencies of low salinity values are still high and act as a negative factor for colonization by species from Kattegatt.

INFLUENCE OF TEMPERATURE

Steemann Nielsen (1951) found in Isefjord, a bay of Kattegatt on the northern part of Zealand, a reduction of the number of benthic species from the entrance to the inner part of the bay. Isefjord has a relatively high and constant salinity of about 18 - 24 o/oo in the whole waterbody. The temperature at summertime could rise to more than 20° C at all depths. Steemann Nielsen maintains that the decrease in the number of species, i.e. Dilsea carnosa, Delosseria sanguinea and Laminaria digitata, depends on these high summer temperatures.

As has been shown on pp. 35 and 37, the difference in annual and monthly mean temperature in Kattegatt and the Öresund is comparatively low. Moreover, the difference in quartiles, quartile range and variation breadth of temperature at the different localities and depths within the Öresund (p. 38) is very small. Therefore, it seems less probable that the large differences in floral composition and

behaviour of the algae, which have been described in section II and in this section, can in the first instance be correlated with the temperature factor alone.

When evaluating the changes of the algal flora in the Öresund area, one has to consider the relation between salinity and temperature. Schwenke (1959) showed that a combination of higher temperatures and lower salinities could be harmful to *Delesseria sanguinea* and *Phycodrys rubens*. Thus, *Phycodrys rubens* was damaged at 8 ‰ at 15 °C. At 20 °C the species was damaged at 10 ‰. *Delesseria sanguinea* seems to be a little less sensitive: at 15 °C harmful effects were not found until 5 ‰. At 20 °C, however, the species was damaged from 7 - 9 ‰. These observations lie near the actual range of temperature and salinity during summertime for the south part of the Öresund. It is, therefore, possible that the temperature may act as a negative factor for the flora in this part of the Sound.

The absence of the *Laminaria* species in the uppermost part of the sublittoral zone in the area south of Kullen could partly be a temperature effect. Sundene (1964) has shown that *Laminaria* species are damaged by temperatures above 20 °C. Similar investigations on *Laminaria* species have been performed by the author on material from the Öresund, which gave the same result. Mature specimens of *Laminaria digitata* and *Laminaria saccharina*, collected at Grällegrund, were cultured in large aquaria with recirculating sea-water of about 15 ‰. The temperature was at the beginning 5 °C and was increased gradually during four months to 21 °C. At about 20 °C all individuals within two days turned green and began to decay.

In some cases the algae seem to be able to change their sensitivity to the salinity - temperature range. Druehl (1967) measured the distribution of *Laminaria saccharina* in relation to salinity and temperature on the west coast of USA. The distribution range for the same species in the Öresund area is much larger (Fig. 127).

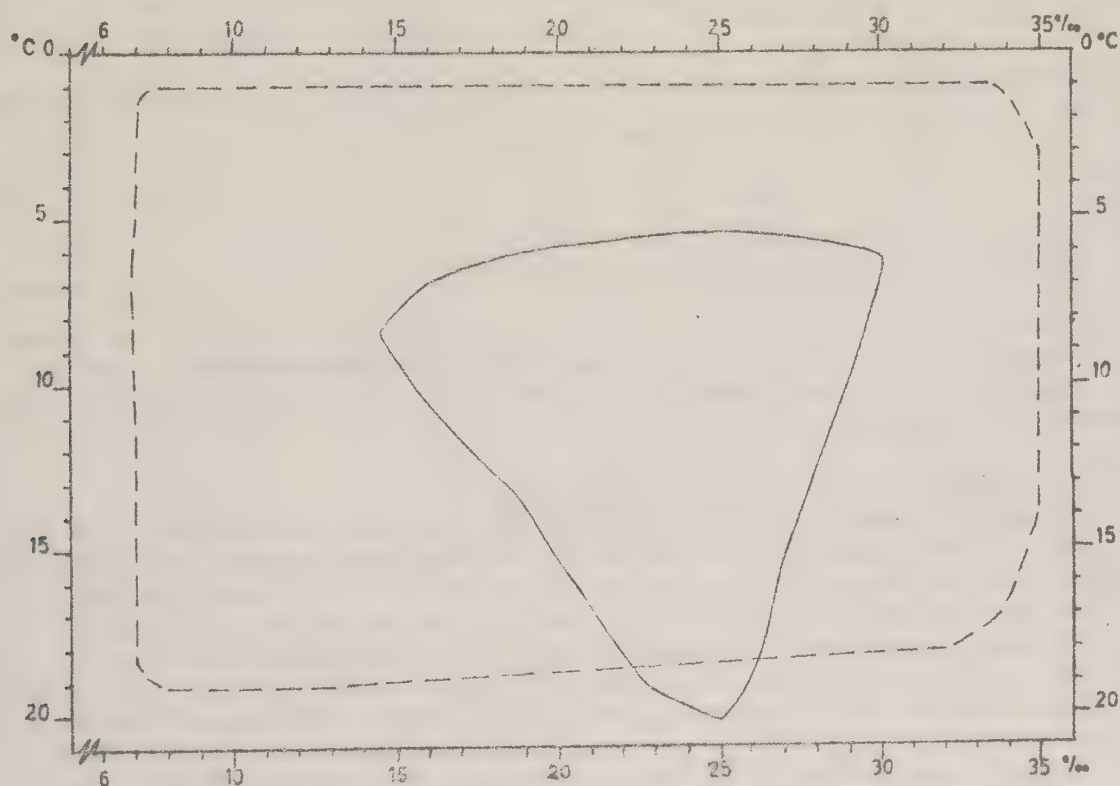


Fig. 127. Distribution range of *Laminaria saccharina* in relation to salinity and temperature in the Öresund area compared with the west coast of USA (Druehl, 1967).

----- Öresund ————— the west coast of USA

A factor which could be important is the large daily variation in temperature of the bottom water in the north and middle part of the Öresund area, especially during summer and winter (p. 41). In January the difference from one day to another can amount to 7 °C and in August to 9.5 °C within two days. The conditions in Kattegatt and the Baltic seems to be more stable. The fluctuating temperature may act as an additional stress factor on the flora in the Öresund area.

The long-term variation in temperature, which has been demonstrated on p.49, with an increase of 0.2 - 0.8 °C at different depths from 1923 to 1939, has according to Brattström (1941, 1947) and Dahl (1946, 1950) resulted in a colonization of several animals, both invertebrates and fishes. The temperature showed high values in 1935-39 and in 1950-52 with another maximum in 1959-61. There is, however, no evidence for a similar change in the algal flora.

The Rhodophyta / Phaeophyta ratio

Feldmann (1938) has pointed out that the ratio Rhodophyta / Phaeophyta increases with temperature. Thus, in arctic waters the ratio should be 1.0 - 1.5, in the English Channel about 1.5 - 2.0, in the Mediterranean 3.0 - 3.5 and in tropical areas 4.0 - 4.5. The Rhodophyta / Phaeophyta ratio for the Öresund area is 1.6. The values for different depths, however, vary considerably. In Table 29 the values from the Öresund area are compared with those given by Lund (1959 b) from Greenland.

Table 29. The Rhodophyta / Phaeophyta ratio at different depths for the Öresund area and for Greenland (Lund, 1959 b).

Depth in m	R / P ratio Öresund	Depth in m	R / P ratio	
			Öresund	Greenland
0 - 5	0.9	0 - 10	1.1	0.4
5 - 15	3.1	10 - 20	4.4	0.7
15 - 27	5.8	20 - 30	7.1	0.7

The higher values obtained in the deeper parts of the Öresund area do not correspond with Feldmann's (loc.cit.) calculations. This indicates that the composition of the algal flora is disturbed due to some other environmental factor than the temperature, most probably the salinity.

Influence of low temperature in the littoral zone

Cold weather in January - March is often but not always combined with low water level due to prevailing N - SE - S winds. During such periods measurements with thermoelements were made continuously in the littoral and supralittoral zone at Kullen. The results show that if the water surface is not covered with ice, the temperature in the littoral and the lowest part of the supralittoral zone is not as low as in the upper part of the supralittoral zone. When e.g. the temperature 10 m above the 0-line is -10 °C or even lower, the temperature around the 0-line up to 1 - 1.5 m above is only -2 °C. But even this temperature is sufficient to kill or damage such species as *Lithothamnion lenormandii*, *Dumontia incrassata*, *Ceramium rubrum*, *Scytosiphon lomentaria* and the *Ulothrix* - *Urospora* sp. Whether this is an effect of the low temperature alone or a combination of this and freeze-drying in connection with low water level in February - March, is not clear.

Effect of ice in the littoral and supralittoral zone

Normally the winters in the investigated area are not cold enough for formation of ice on the water. It has, however, happened some years during the investigation period that ice has covered large parts of the area, e.g. in 1966 and 1969. As a rule one can find ice cover or drifting ice in shallow bays for shorter periods every year. The ice does not seem to play an important role for the algal vegetation. There is hardly any ice-scraping with following denudation of the littoral zone which is a common phenomenon in the Baltic.

More important is the formation of a 1 - 2 cm thick ice cortex in the lower part of the supralittoral zone and in the littoral zone, which is often exposed due to the low water level in winter. This cortex is formed by frozen spray and can cover parts of the belts of *Bangia fuscopurpurea*, *Porphyra linearis*, *Fucus vesiculosus* and *Ulothrix - Urospora* sp. The ice cortex does not seem to be harmful to the algae, if it does not last for a longer period than three weeks. Probably it can even have a positive effect by protecting the algae from desiccation. After about three weeks, however, the algae seem to be in the process of decay.

INFLUENCE OF WATER MOVEMENTS

The influence of water movements on the algal vegetation in the Öresund area can be separated into three factors: influence of currents, change in water level and wave action. In the littoral and the uppermost part of the sublittoral zone it can often be hard to distinguish between the effects of currents and wave action, since these factors may influence the flora in the same way.

Influence of currents

The main effects on the flora can be summarized in five points: transport of diaspores to the area and within the area, transport of nutrients and trace elements, influence on the morphology of the algae, removal of detritus from the algae and transport of free-floating algae.

Transport of diaspores. As has been shown, some algae especially red algae, e.g. *Porphyropsis coccinea*, *Cruoria pellita*, *Corallina officinalis*, *Dilsea carnossa*, *Antithamnion plumula*, *Callithamnion corymbosum* and *Callithamnion tetragonum* are sterile or have a reduced ability to sexual reproduction on the fringe of their distribution area (cf. Fig. 126). To maintain the populations of these species it is most probable that diaspores are transported from Kattegatt and in some cases from the north of the Öresund by south-going currents, which are dominant below the halocline (p. 50). At 15 m in depth south-going currents are found in 58 % of the year and at 23 m in 76 %.

The correctness of the assumption is supported by the appearance of spores of *Derbesia marina* in the deep water in the north part of the Öresund. Individuals of *Derbesia marina* are only found in Bohuslän. Furthermore, *Laurencia pinnatifida* has been found to germinate in large numbers of test plates in autumn in the northern part of the area. The irregular appearance of *Euthora cristata*, *Callithamnion bipinnatum*, *Ceramium penicillatum* and *Polysiphonia brodiaei* at Kullen may also depend on a long transport of diaspores from the northern part of Kattegatt. Thus, the current conditions may be of great importance to maintain the population of the species listed in Fig. 126.

Transport of nutrients and trace elements. As has been shown in section I, there exists a great short-term variation in the content of nutrient salts and trace elements along the coast of the Öresund due to wind and current conditions. This may act as a positive factor for the algal flora, as there is no deficiency of nutrients due to stagnation phenomena. But on the other hand, sudden increases in the trace element level of the water may act as a severe stress factor.

This may explain the impoverishment of the flora in the Barsebäck area, which depending on current directions is affected by polluted water either from the Landskrona or the Malmö area. In Barsebäck there is a decrease in the abundance of several species, e.g. *Scytosiphon lomentaria*, *Fucus serratus*, *Fucus vesiculosus* and *Acrosiphonia centralis*. On some occasions the breakwaters of Barsebäck harbour were quite devoid of algae.

Morphology and growth of the algae. Although it is very hard to distinguish between the effects of currents and waves, especially in the littoral and the uppermost part of the sublittoral zone, it seems probable that changes in these zones depend mainly on wave action. In the deeper parts of the sublittoral zone the current may be of greater importance. The only observed example, where the current conditions seem to be of any real importance for the morphology of the algae is the modification of *Fucus serratus*, known as "*f. grandifrons*", at the threshold area between Malmö and Copenhagen. This "form" has very broad, 5 - 6 cm, and long, 75 - 100 cm, thalli.

Printz (1926) and Jorde & Klavestad (1963) were of the opinion that the algal flora was richer at localities with stronger currents than in adjoining parts in some Norwegian fjords. In the Öresund area no such differences have been observed.

Removal of detritus from the algae. Though the amount of particles in the water of the Öresund is comparatively high (0.25 - 1.00 mg/l according to Hermann, 1967), the sedimentation on the algae is relatively low, at least at depths from 0 - 15 (- 20) m, except in e.g. Lomma Bay and the vicinity of Copenhagen. The absence of a more pronounced detritus cover at these depths must presumably be an effect of the current conditions.

But below 20 m in depth, where the current velocity is markedly reduced from a maximum value of about 150 cm/s at 15 m to about 50 cm/s at 23 m in depth (p. 59), the algae can be heavily coated with detritus, which would reduce the production. Indications of this have, however, not been found. The *Delesseria sanguinea* vegetation in Lomma Bay, for example, which is heavily coated with detritus, seems nevertheless to have a normal growth. This could be explained by the possibility of heterotrophic growth, which has been suggested by i.a. Lund (1959 b) and Wilce (1967).

On the other hand, sedimentation on the bottom may have a negative effect on the germination of spores and zygotes, as they probably cannot germinate on a soft substratum, even if this is very thin. This can be illustrated by the conditions at a locality in the vicinity of Copenhagen. Rosenvinge (1909) refers to the same locality (OG 16/4 1894) between Tre Kroner and Middelgrund. He found a clean bottom with i.a. *Membranoptera alata*, *Phycodrys rubens*, *Desmarestia aculeata* and *Sphacelaria plumosa*. Today the bottom consists of mud and there is no vegetation.

Transport of free-floating algae. Especially during spring there is a very luxuriant growth of mostly confervoid algal species, such as *Ceramium* sp, *Poly-siphonia* sp, *Ectocarpus* sp, *Pilayella* sp, *Desmarestia viridis* and *Cladophora glomerata*. When the specimens reach a certain size, they are detached by wave action or in the case of *Desmarestia viridis* more probably by currents.

A large part of these algal masses will rapidly sink to the bottom and be transported along this by currents. Sometimes they have been observed to gather in strings, which are often seen to be trapped in shallow holes on the bottom or entangled in the normal attached vegetation, causing oxygen deficit. Parts of these algal masses can be transported into shallow waters and washed ashore. The loose-lying and drifting algae can make a large contribution to the algal biomass in the north and central parts of the Öresund. In some areas, e.g. Barsebäck and Lomma Bay, the use of fishing-nets is impossible during spring, as they are filled with algae.

Transport of algae can without doubt cover relatively long distances. Free-floating specimens of *Halidrys siliquosa* are frequently found in the central and south part of the area down to Skanör. Judging from their size they must emanate from areas north of the Öresund.

Change of water level

As stated on p. 51, the water level in the Öresund is to a minor degree affected by tidal phenomena. The major part of the changes in water level is due to the wind and air pressure conditions over the North Sea, Skagerrack, Kattegatt and the Baltic. Prevalent low water occurs mostly during spring from February to April, when the water level can be 0.5 - 0.75 (- 1.0) m below the nor-

mal for long periods. This will affect the littoral and supralittoral zone in several ways.

During such low water periods when low air temperatures, often below zero, are frequent there may be a combined wind-temperature effect (freeze-drying) on the algae. Such damage has been observed to e.g. *Porphyra linearis*, *Porphyra purpurea*, *Porphyra umbilicalis*, *Lithothamnion lenormandii*, *Dumontia incrassata*, *Ceramium rubrum*, *Ceramium strictum*, *Polysiphonia nigrescens*, *Pilayella rupincola*, *Scytosiphon lomentaria* and the *Ulothrix-Urospora* sp. Some years even *Ascophyllum nodosum*, *Fucus spiralis* and *Fucus vesiculosus* are damaged. The effect is enhanced, since during such periods the winds are E - SE - S, which gives no or very little spray and no protecting ice cortex on the Swedish side of the Öresund. Some species, e.g. *Dumontia incrassata*, *Pilayella rupincola*, *Scytosiphon lomentaria* and the *Ulothrix-Urospora* species, can grow out rapidly when the conditions get more favourable probably from surviving basal parts.

Influence of wave action

That the degree of wave action affects both the floral composition and the morphology of the algae is a well-known fact (cf. Schwenke, 1971). In the Öresund area where the maximum height of the waves varies from 1.3 to 3.8 m (p. 53) at different localities, some species e.g. *Porphyra linearis*, *Porphyra umbilicalis*, *Polysiphonia brodiaei*, *Petalonia zosterifolia* and *Chaetomorpha aerea*, are only able to grow at exposed to very exposed localities, while others e.g. *Porphyra purpurea*, *Ascophyllum nodosum*, *Fucus distichus* ssp. *edentatus* and *Monostroma grevillei* can only survive in sheltered positions.

Due to prevailing wind directions and forces during different parts of the year, there are great changes in the composition of the flora in the supralittoral zone. The height above the O-line and the breadth of the different belts seem to be proportional to the degree and frequency of surf exposure (cf. Fig. 128). Thus, in summer there are hardly any algae found in the supralittoral zone except *Rhodochorton purpureum* and *Waerniella lucifuga* in shaded localities with a constant high relative humidity. In autumn, on the other hand, when high water level is prevalent due to a high proportion of strong NW - W winds, the algae can colonize the supralittoral zone, e.g. *Bangia fuscopurpurea*, *Porphyra linearis*, *Petalonia zosterifolia*, the *Ulothrix-Urospora* species, *Blidingia minima* and *Enteromorpha intestinalis*. Some of these species can be found as high as 4 - 6 m above the O-line at exposed localities, e.g. *Bangia fuscopurpurea* and *Porphyra linearis*.

Even in the upper part of the sublittoral zone the vertical distribution of some species, e.g. *Furcellaria fastigiata*, *Ahnfeltia plicata*, *Chondrus crispus*, *Membranoptera alata*, *Rhodomela confervoides*, *Chaetomorpha melagonium* and *Bryopsis plumosa*, is changed towards a somewhat higher position than normal at exposed localities.

In the supralittoral zone there seem to be morphological changes at different distances from the O-line for at least the *Urospora* species. In the upper parts of the belt the filaments are thinner.

The influence on the morphology of the algae in the littoral zone due to the degree of exposure is most dominant in *Fucus serratus* and *Fucus vesiculosus*. On pp. 223, 224 and 227 the variability of *Fucus vesiculosus* has been demonstrated. At very exposed localities the thalli are short and devoid of bladders. This agrees with observations made by Conway (1954). With decreasing degree of surf exposure the *Fucus vesiculosus* thalli get larger and the number and size of air-bladders increase. These modifications have earlier been described as different forms of the species (cf. Kjellman, 1890, Kylin, 1907). The same tendency is observed in *Fucus serratus* which has typical "surf forms". At the most exposed localities in the area *Fucus serratus* is absent or depressed to 5 - 6 m in depth. In the case of the reduced growth of *Fucus vesiculosus* at very exposed localities, besides the mechanical effects of the waves, the increased loss of extracellular exudates may be an important factor.

In an area like the Öresund, which is rather narrow and has a heavy boat traffic with about 40 000 ships passing every year, the swell from these boats may play an important role at least in localities that are sheltered from wave action. An example of this has been observed in the vicinity of the harbour of Copenhagen, where a more or less constant swell from the traffic has changed the zonation pattern of *Fucus distichus* ssp *edentatus* and *Fucus serratus*. Thus, at the entrance of the harbour of Copenhagen *Fucus distichus* ssp *edentatus* is found belt-forming even in the lowest part of the supralittoral zone from 0 - 0.25 m above the 0-line (cf. Fig. 137). Furthermore, *Fucus serratus* is intermingled with *Fucus distichus* ssp *edentatus* and *Fucus vesiculosus* in the littoral zone.

Measurements of wave action

It is very difficult to make an objective measurement of the degree of surf exposure. One always finds more or less vague and subjective statements in the literature, such as "moderately exposed" or "very exposed" localities. These terms will of course vary from author to author, depending on his experience. Lewis (1964) states that "in the face of all these variations it seems doubtful if categories of exposure can ever be expressed except in words". He, therefore, defines very exposed and sheltered localities by giving type localities. Grenager & Baardseth (1966) made an attempt to describe the degree of exposure in different localities by using a transparent circle with sectors of 90° with the radius equal to 7.5 km. The number of open sectors without land or ground is equal to the exposure. This method, however, does not consider, e.g. prevailing wind directions, and it will not give correct values in an open archipelago.

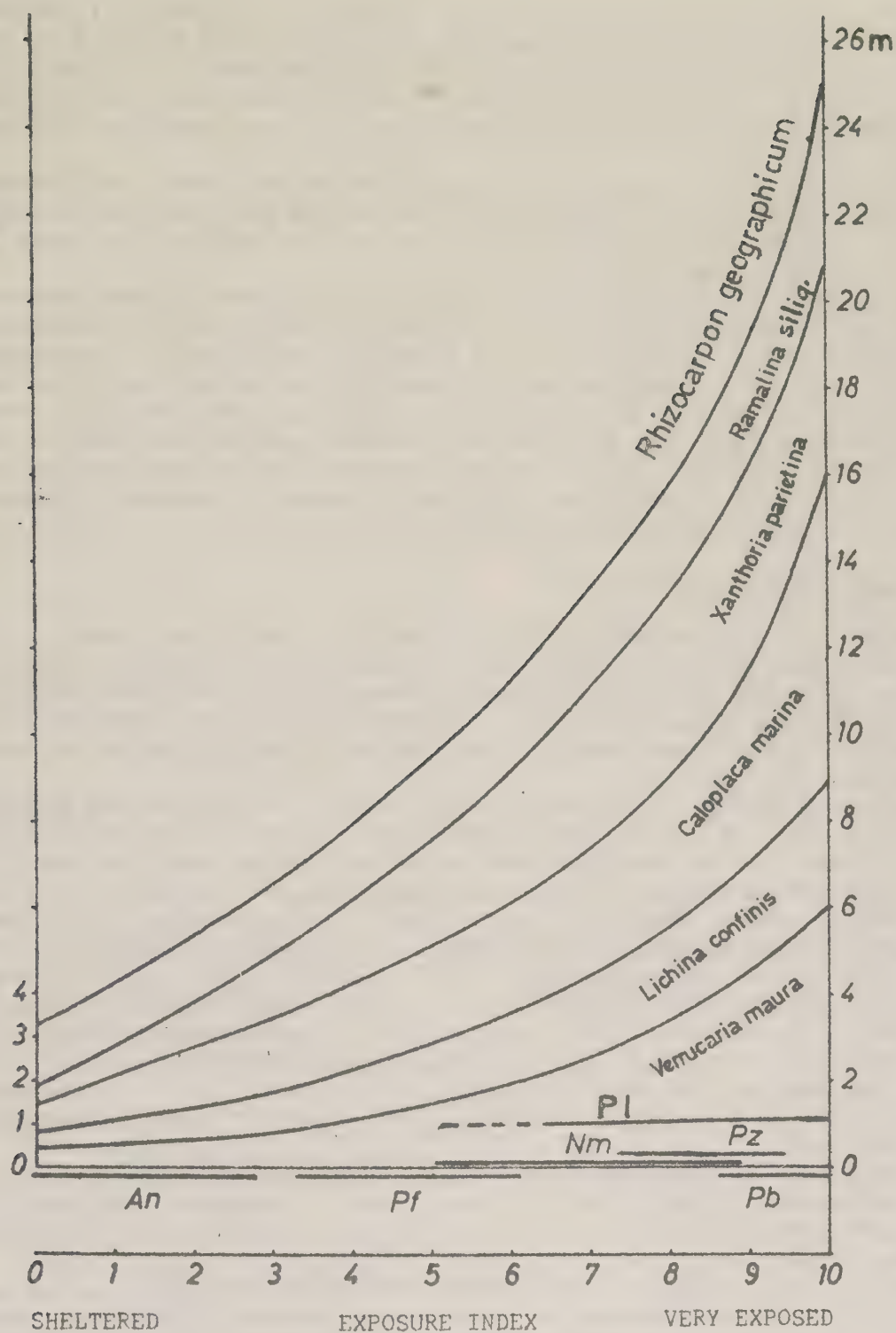
The author is of the opinion that by means of a combination of the zonation and breadth of the lichen belts in the supralittoral zone and certain indicator algae from the littoral zone, it should be possible to get a relative scale of the degree of exposure in a locality. This is illustrated in Fig. 128. There are, however, many difficulties to be overcome before this system could be used in larger areas, e.g. the differences between tidal areas and areas without tide. The choice of indicator algae is important. Most of the possible indicator algae may have a restricted distribution and behave differently in different parts of their distribution area, e.g. *Ascophyllum nodosum*. The angle between the shore and the water has also to be considered. The breadth of the different lichen zones, the black, orange, yellow and grey, is probably more constant over large areas.

The lichen zonation

As a complement to Fig. 128 a short description of the zonation of lichens in the supralittoral zone of the area will be given. Just above the upper limit of the *Balanus* belt there is a black zone of *Verrucaria maura*. The vertical distribution of this and the degree of cover can vary considerably depending on insolation and the degree of exposure. In semi-exposed sunny localities the *Verrucaria* belt is only seen as small patches. In very exposed localities the lower parts of the *Verrucaria* belt are replaced by blue green algae, mainly *Calothrix scopulorum*, *Entophysalia deusta*, *Lyngbya lutea* and *Phormidium coleum*.

The breadth of the *Verrucaria* belt varies with the degree of exposure. Söderström (1965) reports an elevation of 5 m on very exposed skerries in the outer archipelago of Bohuslän. On Hallands Väderö the present author has measured the elevation of the *Verrucaria* belt to maximally 5.5 m above the 0-line, whereas Almborn (1955) gives the breadth as only 1 m. At Kullen the black zone varies from 0.5 - 4 (- 6) m. In the rest of the Öresund the breadth varies from 0.2 - 1 m. The black zone in the Baltic seems to be more narrow even in very exposed localities, compared with the west coast of Sweden. This could indicate that the salinity plays a role in the elevation of the black zone in the Baltic.

In the upper part of the *Verrucaria* belt one can regularly find small patches of *Lecanora helicopis*. *Lichina confinis* is found in a transitional zone between *Verrucaria maura* and the orange belt, which consists mainly of *Caloplaca marina*. This orange belt is succeeded with a relatively sharp border by a bright



Nm=*Nemalion multifidum*, Pz=*Petalonia zosterifolia*:

An=*Ascophyllum nodosum*, Pf=*Petalonia fascia*

Pb=*Polysiphonia brodiaei*, Pl=*Porphyra linearis*

Fig. 128. Scheme for estimation of exposure indices.

yellow belt of *Xanthoria parietina*. On the border to the grey belt, which mainly consists of *Lecanora atra*, one can also find *Anaptychia fusca*. At this level the first sign of *Ramalina siliquosa* is also found on vertical cliffs. The *Lecanora atra* belt is a little higher up succeeded by *Rhizocarpon geographicum* and the upper limit of the supralittoral zone is set to the lower limit of *Parmelia saxatilis*.

Empirically it has been found that with winds of about 10 m/s after 4 - 5 hours the surf reaches the lower limit of the orange belt (*Caloplaca marina*) and with winds of about 14 m/s after 4 - 5 hours the surf reaches the lower limit of the yellow belt (*Xanthoria parietina*).

This schematic review of the lichen zonation differs in one respect from what is found by Almborn (loc.cit.) at Hallands Väderö and by Eliasson (1965) from Bohuslän, namely the occurrence of *Xanthoria parietina* in a continuous belt at suitable localities along the entire coast of the Öresund except at Hallands Väderö and Hovs Hallar. On other parts of the Swedish coast one finds the species only on bird droppings. Both Eliasson and Almborn consider the species to be ornithocoprophilic. The explanation of these phenomena may be the increased level of nutrient salts in the Öresund area (cf. the increased occurrence of *Rosenvingiella polyrhiza* and *Prasiola stipitata* in the Öresund).

INFLUENCE OF LIGHT CONDITIONS

The light conditions may affect the benthic algae in many ways, e.g. the vertical distribution, the growth rate and the formation and release of gametes and spores. The different light effects are probably also linked with temperature, salinity, availability of nutrients etc. The combined light and temperature conditions are probably of great importance for the changes in aspect during the year, as is shown in Figs. 131 - 138.

The growth periods for some algae in relation to temperature and light are shown in Fig. 129. The relatively constant start of the growth of *Monostroma grevillei* from year to year has been studied in the Öresund area for about ten years. It seems that growth starts at nearly the same time, in February, even if the water temperature varies from year to year. Thus, the increasing light intensity may be the main triggering factor for the start of growth. This hypothesis is strengthened by finds of *Monostroma grevillei* at 6 - 8 m in depth not until the middle of March. These specimens were delayed in their development by about one month. Specimens growing at the normal depth were ca 5 - 10 cm in length, while specimens at 6 - 8 m in depth were only 1 - 3 mm in length. The temperature at the two depths was about the same but the available light at the greater depth was reduced. Similar observations have been made concerning the growth of *Dumontia incrassata* at 8 - 12 m in depth.

Another find of *Monostroma grevillei* illustrates the same thing. A population of the species in the mouth of a small crevice showed at the same time a gradient of development in relation to light. In full sun-light the specimens were 12 cm long, while they at the most shaded position were only 1 - 2 mm.

The light conditions in the Öresund have probably changed during recent years (p. 105) and the compensation depth for phytoplankton may have decreased (Edler, 1973). There are, however, no indications of this for the benthic algae. It is also very difficult to judge from field observations if the production rate for benthic algae in the lower part of the sublittoral zone has decreased, as there are no previous measurements to compare with. The lower border for benthic vegetation in the area is found at about 25 - 27 m in depth, which coincides quite well with the 1 % level of light.

According to i.a. Levring (1947) the spectral composition of the light and the light intensity is responsible for the composition of the algal vegetation at different depths. The distribution of the different algal divisions at different depths is shown in Table 30.

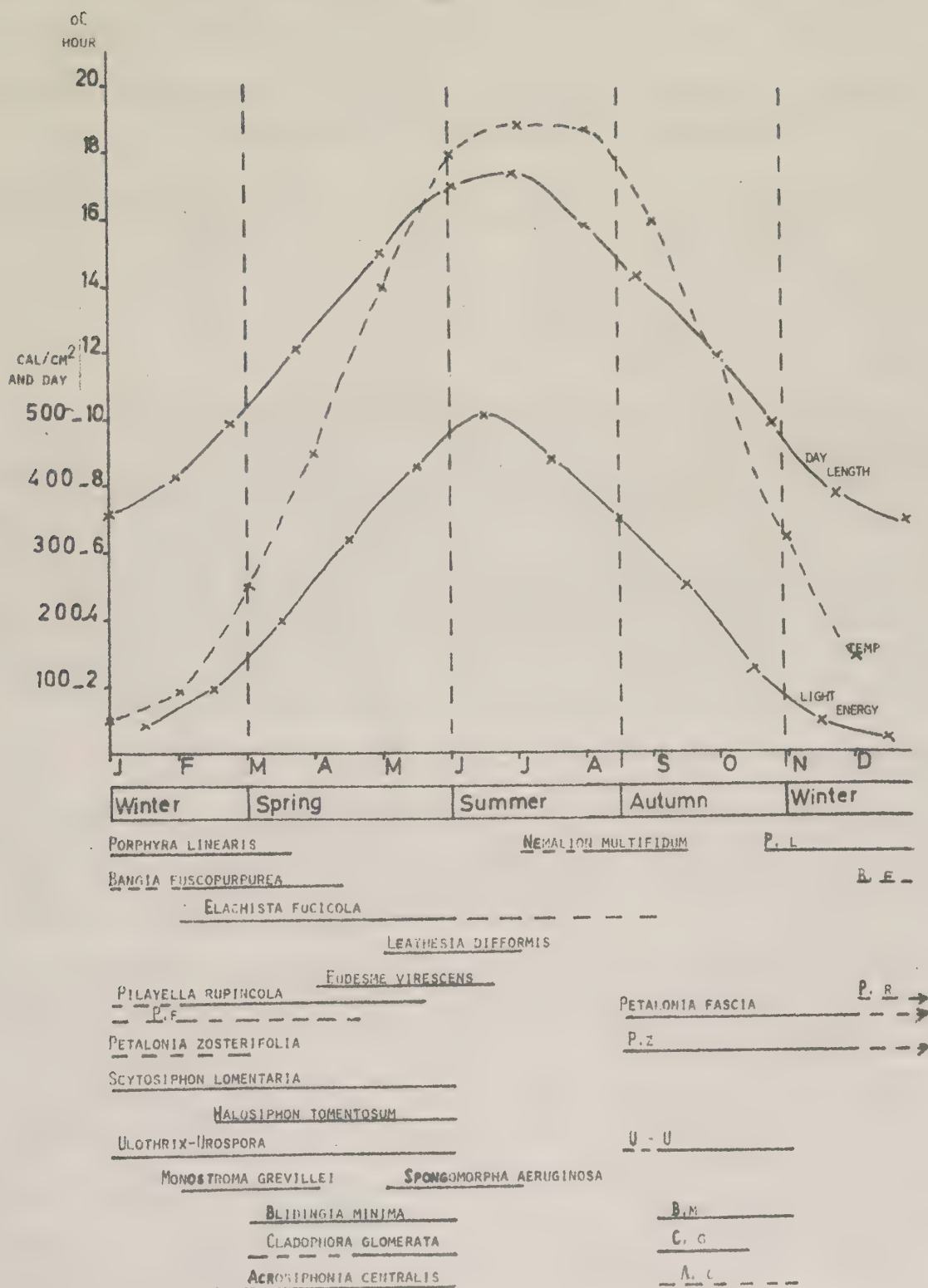


Fig. 129. Growth periods for some algae in the north part of the Öresund in relation to temperature, light intensity and day length.

Table 30. Number and percentage of species of the three algal divisions at different depths in the Öresund area.

Depth	Rhodophyta		Phaeophyta		Chlorophyta		Σ n
	n	%	n	%	n	%	
0 - 5 m	51	32	57	36	52	33	160
5 - 15 m	69	63	22	20	18	17	109
15 - 27 m	69	80	12	14	5	6	86

The number of green algae decreases rapidly at greater depths. In the lowermost part of the sublittoral zone the proportion of green algae is only 6 %. The same tendency is found among the brown algae though not so drastic. The proportion of red algae on the other hand increases with greater depth from 32 to 80 %.

Especially in connection with the vertical distribution of the red algae there may be an interaction between salinity and light conditions. As shown in Fig. 124 many red algae change their vertical distribution due to changes of the salinity. But this downward process may be limited by the light conditions at greater depths. Some species are probably more light-demanding and, therefore, only found in the littoral zone and do not seem to be able to change their vertical distribution. Such species are e.g. the *Porphyra* species, *Nemalion multifidum*, *Ceramium penicillatum*, *Polysiphonia brodiaei* and *Chaetomorpha aerea*.

CHANGES IN ASPECT

As described in section II, there are marked changes in the composition of the algal flora during the year, especially in the supralittoral and littoral zone and to a lesser extent in the sublittoral zone. These changes in aspect are only in a few cases bound to salinity changes but are most likely correlated with changes in temperature, light conditions, a combination of temperature and photoperiod and to some extent changes in water level.

The aspect changes are most prominent in the northern part of the area but are also found in the southern part. In the northern part one can distinguish four different aspects, viz. winter, spring, summer and autumn (Fig. 129), while in the southern part only three aspects are recognizable. The change between these aspects is of course "fluent" but in a wider context the changes are astonishingly synchronized. The beginning of growth and the growth period are relatively constant for many species, varying from 1 - 2 weeks between different years. The changes in aspect are illustrated in Figs. 131 - 138.

The following description refers to the northern part of the Öresund from the supralittoral to the uppermost part of the sublittoral zone.

The winter aspect as a rule begins in the end of October or the beginning of November and lasts to the middle or the later part of February. This period is characterized by decreasing light intensity from about 75 cal/cm² and day in November to about 35 in December and increasing to 140 in the end of February (cf. Fig. 129). The day length from sunrise to sunset varies from 9.5 - 7 - 10 hours, the temperature from 6.5 - 1 - 5 °C. Winds from NW - W - SW, often of higher forces, dominate together with higher water level in November - December.

In the supralittoral zone the growth of *Porphyra linearis* begins. The species often reaches its maximum size within 2 - 3 weeks time. The *Porphyra linearis* belt reaches its maximum extension in December. The first sign of the *Bangia fuscopurpurea* belt is found. The growth of *Blidingia minima* and *Enteromorpha intestinalis* in the supralittoral zone begins. The *Petalonia fasciata* and *zosterifo-*

lia belts now become fully developed. In the littoral zone the growth of *Ceramium rubrum* and *Ceramium strictum* is vigorous. In the sublittoral zone there seems to be very little activity.

The winter aspect ends in the later part of February, when most of the species mentioned begin to decay or dry as a result of the prevalent spring low water, though single specimens of the winter aspect can survive for another month. The winter aspect is thus characterized by a few species, which have a relatively high degree of cover.

The spring aspect begins at the end of February or the beginning of March and lasts to about the end of May or the beginning of June. This period is first characterized by low temperature from about 5°C (-1°C during night) to 9°C , often low water level and increasing light intensity from about 150 to 250 cal/cm^2 and day. In the later part of the spring aspect the water level is normal. The temperature increases rapidly to $16 - 18^{\circ}\text{C}$ and the light intensity to $425 - 475\text{ cal/cm}^2$ and day. The day length increases during the whole period from 10 to 17 hours.

In the supralittoral zone the *Porphyra linearis* belt is succeeded in its uppermost part by a *Bangia fuscopurpurea* belt and in its lower part by the green *Ulothrix-Urospora* belt. In the littoral zone the growth of *Dumontia incrassata*, *Scytosiphon lomentaria*, *Chorda filum*, *Monostroma grevillei* and *Acrosiphonia centralis* is vigorous. In more exposed localities *Pilayella rupincola*, *Halosiphon tomentosum* and *Spongomorpha pallida* appear.

During the spring aspect many of the very small epiphytical red, brown and green algae, such as *Acrochaetium polyblastum* and other *Acrochaetium* species, *Hecatonema* sp, *Microspongium globosum*, *Myrionema corunnae* and *Pseudopriingsheimia fucicola* develop rapidly. The epiphytical algae *Ceramium arborescens*, *Ceramium rubrum*, *Ectocarpus* sp, *Elachista fucicola* and *Pilayella littoralis* have a luxurious growth. Species like *Chordaria flagelliformis*, *Eudesme virescens*, *Desmotrichum undulatum*, *Ulvaria oxysperma* and *Rosenvingiella polyrhiza* can also be added to the spring aspect. In the sublittoral zone the growth of *Ceramium rubrum*, *Polysiphonia fibrillosa*, *Polysiphonia urceolata* and *Polysiphonia violacea* is considerable.

The spring aspect is characterized by comparatively many species with high growth rate. The transition to the summer aspect begins in the middle or the end of May, when many of the spring algae disappear, e.g. *Dumontia incrassata*, *Scytosiphon lomentaria*, *Halosiphon tomentosum*, the *Ulothrix-Urospora* species, *Acrosiphonia centralis* and *Spongomorpha pallida*, and many of the summer species begin to develop.

The summer aspect begins in the first part of June and lasts to the middle of August. This period is characterized by temperatures between 18 and 19°C , normal water level, moderate wave action, high but somewhat decreasing light intensity from about 500 (max. 515) to 350 cal/cm^2 and day and a day length from 17 (max. 17.5) to 15 hours.

The development of the summer aspect is often very rapid. Many of the species have begun their growth in the later part of the spring aspect. The growth of the summer aspect is luxurious, e.g. *Porphyra purpurea*, *Acrochaetium macula*, *Polysiphonia brodiaei*, *Dictyosiphon foeniculaceus*, *Desmareestia viridis*, *Cladophora glomerata*, *Cladophora glaucescens* and *Spongomorpha aeruginosa*. The latter three species culminate in June and are then detached. In the sublittoral zone *Callithamnion corymbosum*, *Callithamnion tetragonum* and *Broggiartella byssoides* reach their maximum development, though they are found already in spring.

The autumn aspect begins in the first or middle part of August and ends in the later part of October. It is characterized by increasing water level, decreasing temperatures from about 18 to 7°C , decreasing light intensity from about 350 to 75 cal/cm^2 and day and decreasing day length from 15 to 10 hours.

During the autumn aspect *Nemalion multifidum*, which has begun its growth during the summer aspect, grows vigorously. *Porphyra umbilicalis* is maximally developed and fertile. *Cladophora glomerata*, which has survived the later part of the summer as small yellow cushions, begins to grow again. The green *Ulothrix-Urospora* belt is found again but not so luxuriant as during the spring aspect. *Blidingia*

minima, *Prasiola stipitata* and *Rosenvingiella polyrhiza* retain their growth. Both *Petalonia fascia* and *Petalonia zosterifolia* begin their growth in August and thus are a constituent of the autumn aspect even if they also belong to the winter aspect.

In the southern part of the Öresund area only three aspects can be recognized from the supralittoral to the uppermost part of the sublittoral zone due to the impoverishment of the flora and the effect of the strongly fluctuating salinity.

The spring aspect consists mainly of *Pilayella rupincola*, *Scytosiphon lomentaria*, *Monostroma grevillei* and *Acrosiphonia centralis* and in the later part even *Eudesme virescens* and *Desmotrichum undulatum*. Also a few small specimens of *Dumontia incrassata* may be found.

The summer aspect is characterized by a luxuriant growth of *Enteromorpha intestinalis* and *Cladophora glomerata*. The *Ulothrix-Urospora* belt seems to have a delayed development in the southernmost part and is found in the late spring and early summer aspects. In the sublittoral zone *Ceramium strictum* (or *Ceramium tenuicorne*) and *Cladophora rupestris* have a high growth rate.

The autumn aspect is here only noticeable as a poorly developed *Ulothrix-Urospora* belt. In the sublittoral zone there is a marked growth of *Polysiphonia violacea* during October and November.

The winter aspect is lacking or very poorly developed. Many of the species in the area are in bad condition and the dominant *Ceramium strictum* / *tenuicorne* belt is partly decaying.

The changes in aspect in the central part of the area can be said to represent transitional stages between the northern and southern part of the area due to the different south borders of the species.

- | | |
|---|---|
| ★ <i>Acrosiphonia centralis</i> | ○ <i>Lichina confinis</i> |
| ◐ <i>Ahnfeltia plicata</i> | ⊙ <i>Monostroma grevillei</i> |
| //// <i>Bangia fuscopurpurea</i> | ▼ <i>Nemalion multifidum</i> |
| ▲ <i>Blidingia minima</i> | △ <i>Petalonia fascia</i> |
| ≡ <i>Caloplaca marina</i> | • <i>Petalonia zosterifolia</i> |
| ● <i>Calothrix scopulorum</i> | // <i>Pilayella rupincola</i> |
| ▼ <i>Ceramium rubrum</i> | ⊔ <i>Polysiphonia urceolata</i> |
| △ <i>Ceramium strictum</i> | □ <i>Porphyra linearis</i> |
| --- <i>Chaetomorpha aerea</i> | □ <i>Porphyra umbilicalis, purpurea</i> |
| ★ <i>Chordaria flagelliformis</i> | ▲ <i>Prasiola stipitata</i> |
| ▲ <i>Cladophora</i> sp. | ● <i>Rhodomela confervoides</i> |
| ⊕ <i>Dictyosiphon foeniculaceus</i> | ⊙ <i>Rosenvingiella polyrhiza</i> |
| ⊙ <i>Dumontia incrassata</i> | ♦ <i>Scytosiphon lomentaria</i> |
| • <i>Enteromorpha intestinalis</i> | • <i>Spongomorpha pallida</i> |
| □ <i>Fucus distichus</i> ssp <i>edentatus</i> | <i>Ulothrix-Urospora</i> |
| ☆ <i>Fucus serratus</i> | \\ <i>Verrucaria maura</i> |
| ▼ <i>Fucus vesiculosus</i> | • <i>Xanthoria parietina</i> |
| ⊙ <i>Fucellaria fastigiata</i> | ☪ <i>Zostera marina</i> |

Fig. 130. Explanation of symbols used in the vegetation profiles (Figs. 131 - 138).

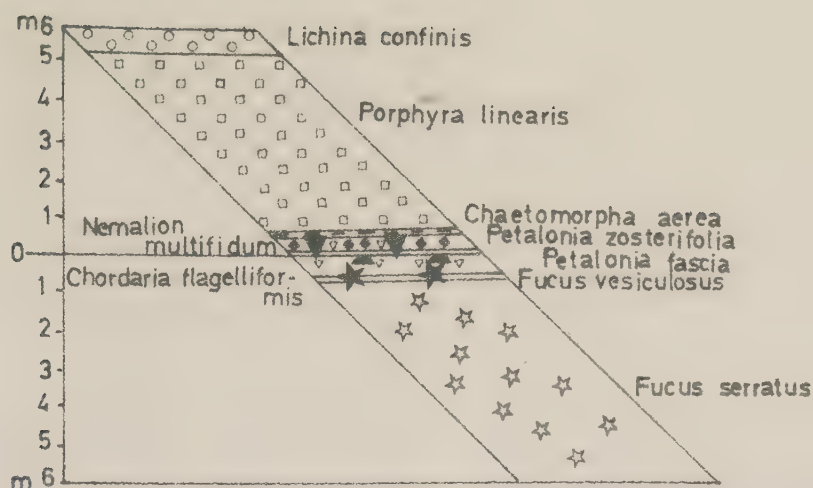


Fig. 131 A. Hallands Väderö 5/1 1966.

The locality is situated on the NW part of the island. The substratum is rock, highly exposed from NE-SW, exposure index 9 (cf. Fig. 128) with an inclination of about 45° . The *Porphyra linearis* belt has its maximum extension and completely covers the substratum from about +0.5 to +5 m. Just below this belt there is a ca 1.5 dm broad but distinct belt of *Chaetomorpha aerea* with specimens ca 2-5 cm long. From about +0.2 to +0.4 m there is a dense belt of *Petalonia zosterifolia*. From the 0-line to +0.2 m scattered specimens of *Nemalion multifidum* in rather bad condition are found. This is the only find of *Nemalion multifidum* later than October in the northern part of the area. The *Nemalion* plants were intermingled with *Fucus vesiculosus* & *compressus* f. *racemosa*. Just below the 0-line there is a well-developed belt of *Petalonia fascia* growing together with *Fucus vesiculosus*. From -0.1 to -0.2 m there is a dense belt of *Fucus vesiculosus* with small bladders downward succeeded by a belt of old *Chordaria flagelliformis* in rather bad condition. The *Fucus serratus* belt is found from -1 m down to about -6 m.

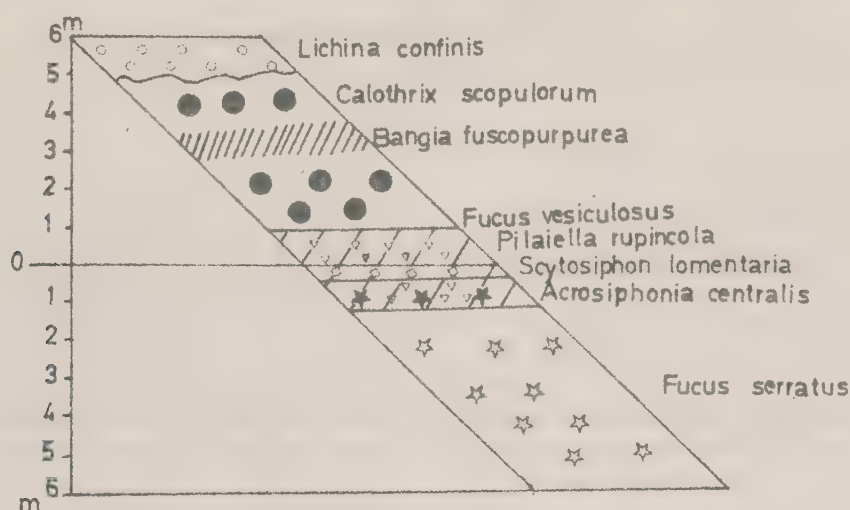


Fig. 131 B. Hallands Väderö 20/5 1966.

Same locality as above. The *Porphyra linearis* belt is succeeded by a *Calothrix* belt with a distinct zone of decaying *Bangia fuscopurpurea* between +2.5 and +3.5 m. The *Petalonia zosterifolia* belt has disappeared and a dense belt of *Pilaiella rupincola* is found growing from +1 m to about -1.5 m intermingled with surf forms of *Fucus vesiculosus*. Just below the 0-line there is a well-developed *Scytosiphon lomentaria* belt about 2 dm in breadth with single specimens of *Spongomorpha pallida*. In the lower part of the *Pilaiella* belt there is a well-developed *Acrosiphonia centralis* belt with young specimens of *Chordaria flagelliformis*. Note the absence of the *Ulothrix-Urospora* belt probably due to competition from *Pilaiella rupincola*.

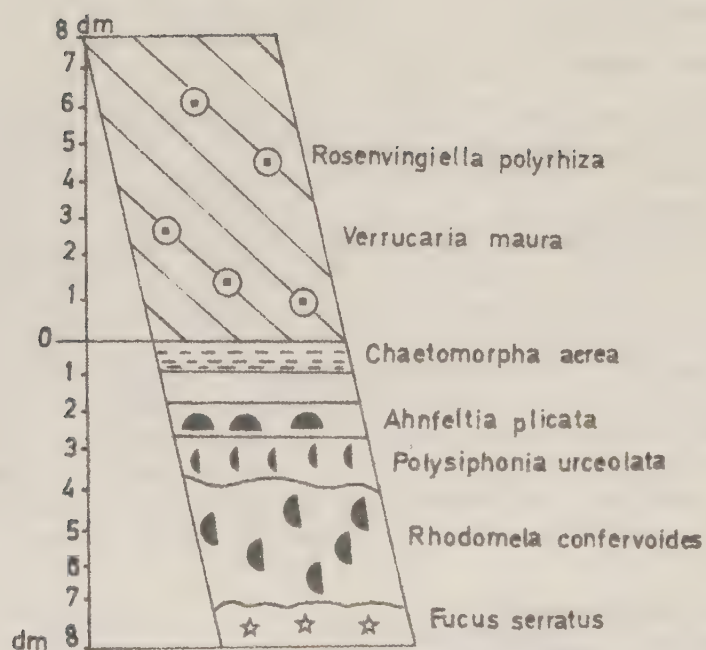


Fig. 132. Ablahamn 24/6 1967.

The locality is situated on the north side of Kullen, substratum rock, exposed from W-NW, exposure index about 4-7, inclination about 80° . The Verrucaria belt extends from the 0-line to about +2 m, more or less covered with *Rosenvingiella polyrhiza*. Just below the 0-line there is a narrow belt of *Chaetomorpha aerea*, dense and well developed. The *Ahnfeltia plicata* zone is found around -2 dm. From -2.5 to -4 dm there is a dense *Polysiphonia urceolata* belt succeeded by a *Rhodomela confervoides* belt with some single patches of *Polysiphonia urceolata*. This belt becomes intermingled or overgrown by *Fucus serratus* from about -7 dm and downwards.

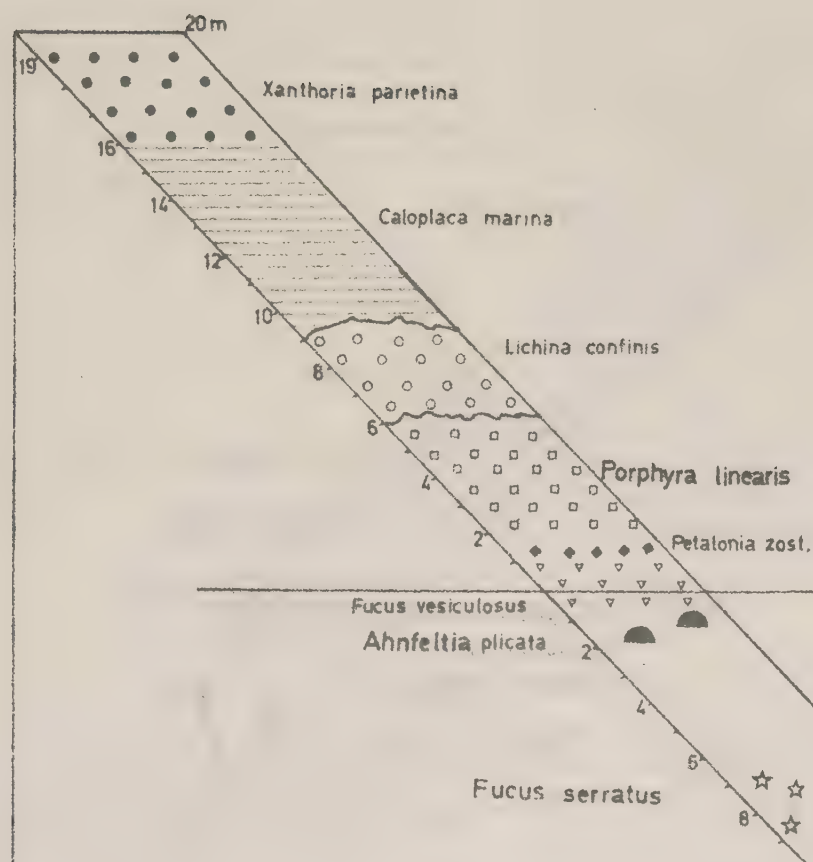


Fig. 133 A. Åkersberget 20/2 1968.

The locality is situated just south of the apex of Kullen. The substratum is rock, highly exposed from N-SW, one of the most exposed localities in the Öresund area, exposure index 10, with an inclination of about 50° . The *Porphyra linearis* belt has its upper limit at +6 m, the lower limit at +2 m. At this height it is succeeded by a rather narrow but dense belt of well-developed *Petalonia zosterifolia*. The *Fucus vesiculosus* belt is found from +0.9 to -0.5 m and consists of small bladderless surf forms. From +0.5 to -0.5 m there are small tufts of very torn *Ahnfeltia plicata* cushions. A more dense belt of the species is found from -1 to -2 m. From -2 to -6.5 m no vegetation was found. The *Fucus serratus* belt does not appear until -6.5 to -7 m.

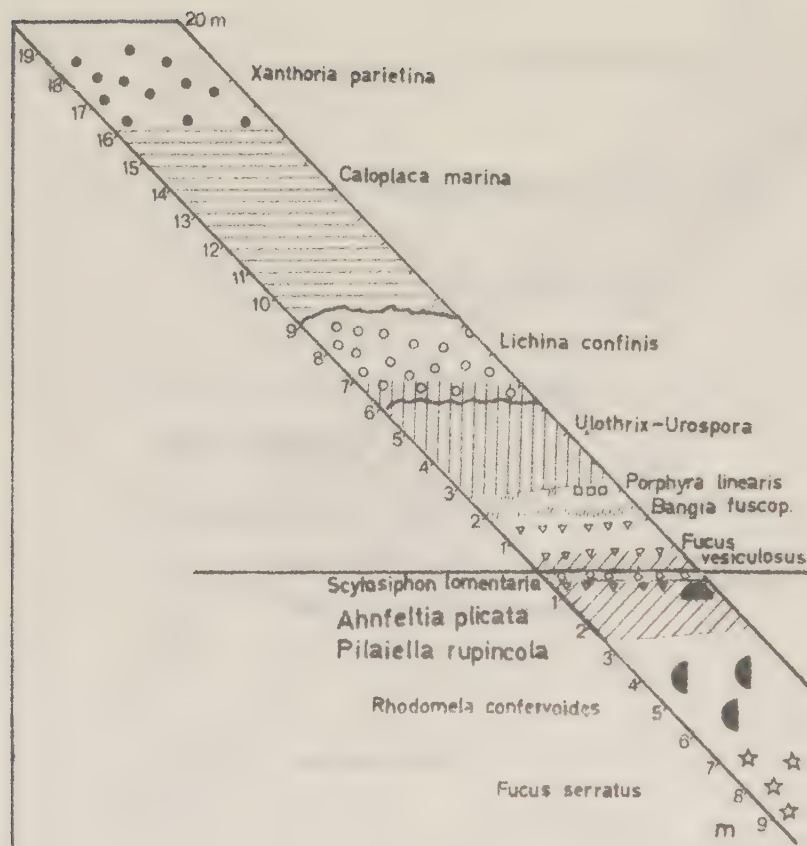


Fig. 133 B. Åkersberget 20/6 1967.

Same locality as above. From +6 to +1 m a dried belt of *Ulothrix-Urospora* is found. In the lower part of this belt there are patches of *Bangia fuscopurpurea* and a few specimens of *Porphyra linearis*. The *Fucus vesiculosus* belt has expanded from +0.9 to +1.5 m. There is a dense *Pilaiella rupicola* belt between +0.75 and -2.5 m. Just below the 0-line there is a narrow belt of *Scytosiphon lomentaria*. The *Ahnfeltia plicata* belt is absent apart from some small patches. The lower part of the *Pilaiella* belt is intermingled with small patches of *Spongomorpha pallida*. In the almost naked zone from -2.5 to -7 m small scattered tufts of *Rhodomela confervoides* are found.

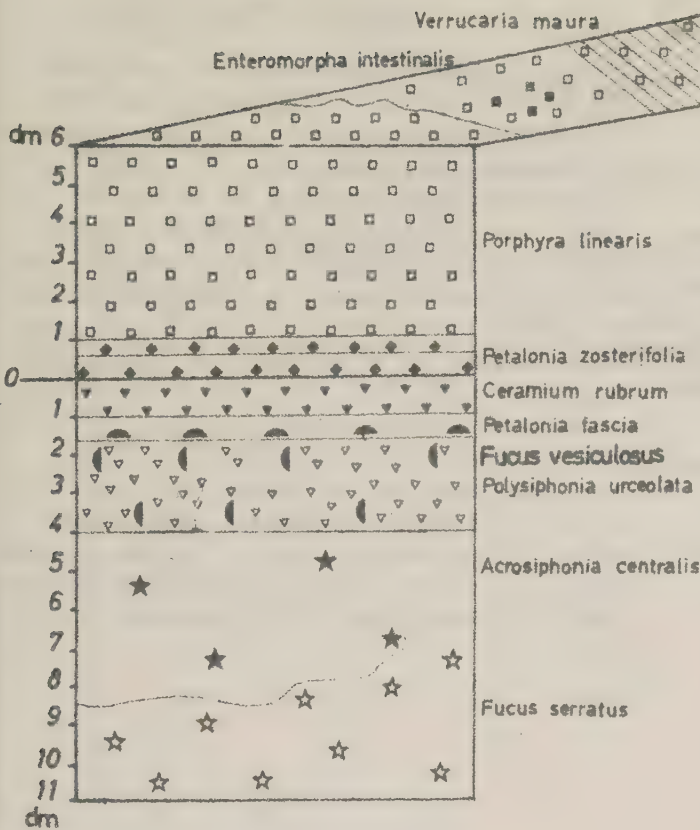


Fig. 134 A. Ransvik 15/2 1968.

The locality lies on the south side of Kullen. The substratum is rock, exposed from W-S, exposure index about 3-6, inclination 90° and then 180° . The *Porphyra linearis* belt has a range from +1 to +6 dm and then 4 m inwards along the horizontal surface. Near the edge there are patches of *Enteromorpha intestinalis*. From the 0-line to +1 dm there is a small belt of *Petalonia zosterifolia*. Just below the 0-line to -1 dm there is a partly killed *Ceramium rubrum* belt with small specimens of *Fucus vesiculosus*. From -1 to -1.5 dm there is a *Petalonia fascia* belt. Below this a *Polysiphonia urceolata* belt consisting of very small scattered cushions with very low degree of cover extends down to about -4 dm. The following zone has young stages of *Acrosiphonia centralis* down to about -6 to -8 dm. Single specimens of *Polysiphonia nigrescens* were also found here. The *Fucus serratus* belt begins at -6 to -8 dm and has its lower border at about -6 m.

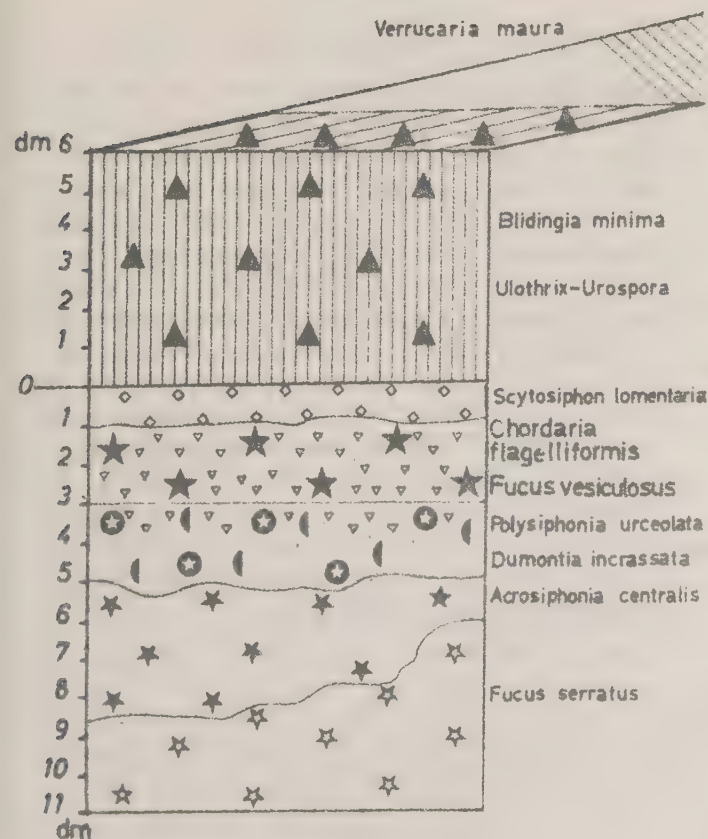


Fig. 134 B. Ransvik 10/6 1966.

Same locality as above. A completely dried *Ulothrix-Urospora* belt with numerous patches of *Blidingia minima* most of which are dead. Just below the 0-line there is a dense and distinct, partly decaying belt of *Scytosiphon lomentaria*, heavily overgrown by different epiphytes. Here also are scattered specimens of *Fucus vesiculosus*. From -1 to -3 dm there is a well-developed and healthy belt of *Chordaria flagelliformis*. Below this from -3 to about -5 dm there is a dense *Dumontia incrassata* belt which has begun to decay, with an undergrowth of *Polysiphonia urceolata*. The *Acrosiphonia centralis* belt is very dense with a high degree of cover, though it has begun to decay.

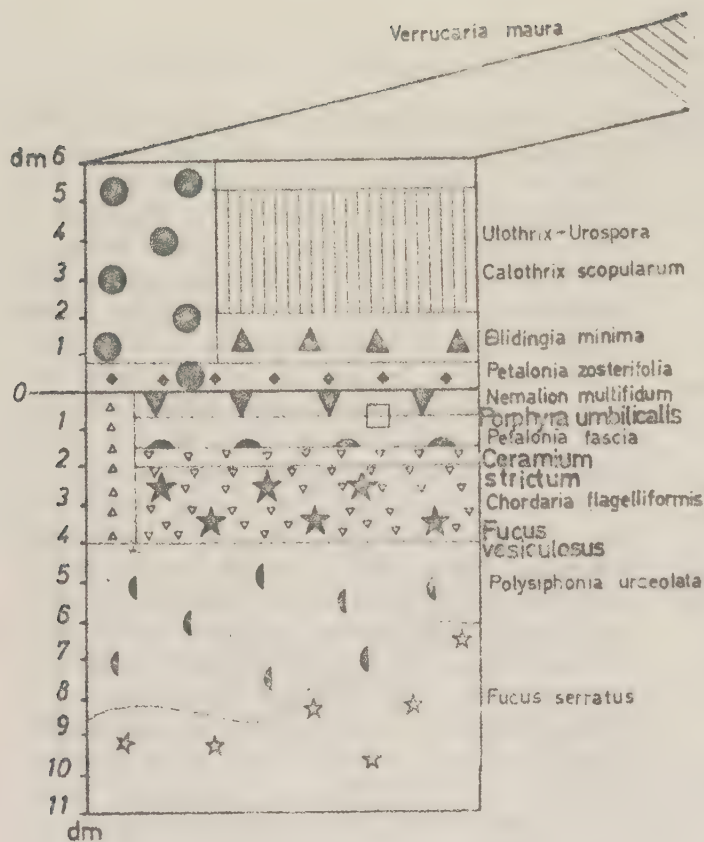


Fig. 134 C. Ransvik 27/8 1966.

Same locality as above. The zone from the 0-line to +6 dm is mostly covered with blue-green algae (*Calothrix scopularum*) with patches of old dead *Ulothrix-Urospora*. Between +1 to +2 dm there are patches of vigorously growing *Blidingia minima*. In the range 0 to +1 dm there are small new specimens of *Petalonia zosterifolia*. Just below the 0-line there is a narrow but dense and luxurious *Nemalion multifidum* belt with patches of *Porphyr a umbilicalis*. At about -1.5 dm small specimens of new *Petalonia fascia* are found and from -2 to -4 dm there is a rather worn *Chordaria flagelliformis* belt. In the range from 0 to -4 dm there are scattered specimens of well-developed *Ceramium strictum*.

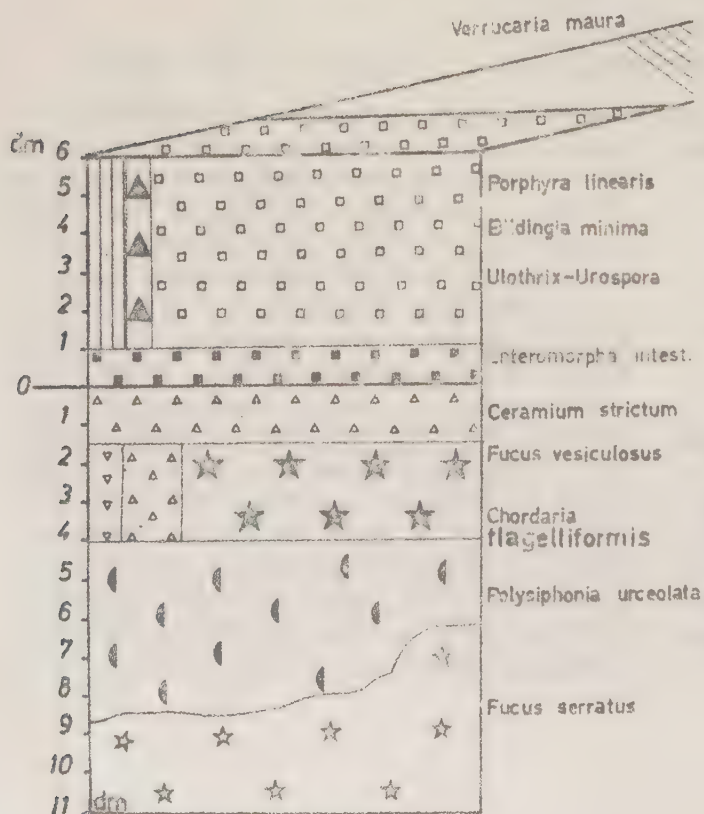


Fig. 134 D. Ransvik 2/11 1966.

Same locality as above. From +1 to +8 dm there is a mixture of young specimens of *Porphyra linearis*. This belt has not yet reached its maximum range. The belt is intermingled with *Ulothrix-Urospora* sp and *Blidingia minima*. The zone 0 to +1 dm is covered with a dense and vigorously growing *Enteromorpha intestinalis* which covers the *Petalonia zosterifolia* specimens. From 0 to -4 dm there is a *Ceramium strictum* belt: Some specimens of *Polysiphonia nigrescens* were also found here. The *Chordaria flagelliformis* belt is beginning to be torn away. Below this zone from -4 to -7 dm the *Polysiphonia urceolata* belt is also in bad condition.

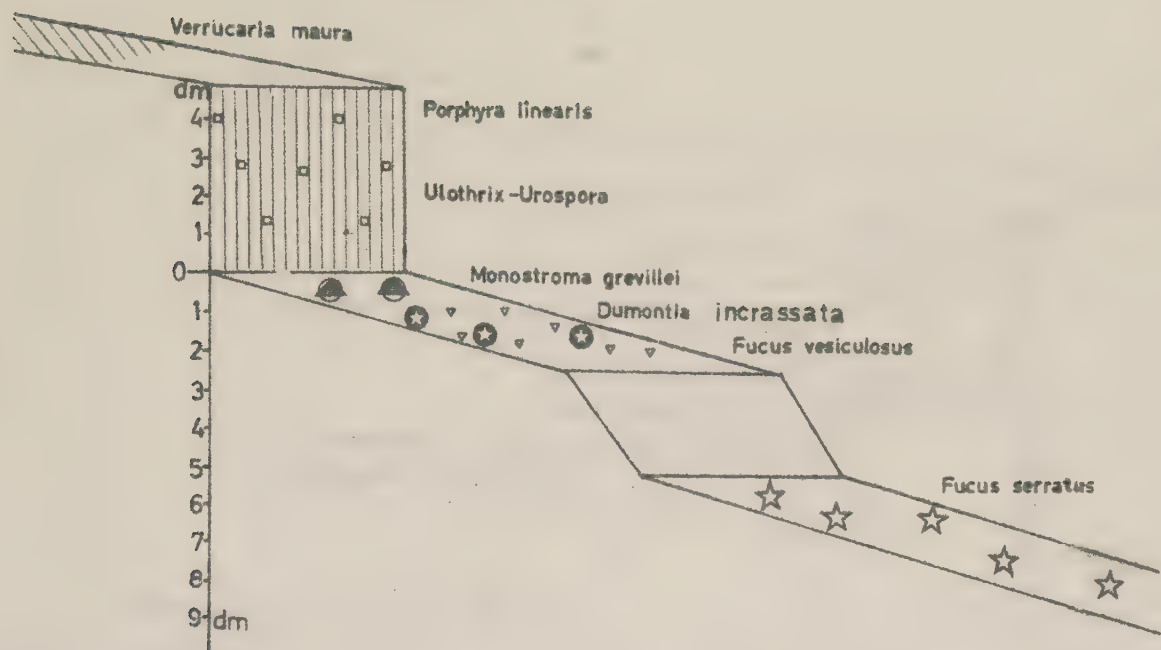


Fig. 134 E. Ransvik 10/3 1964.

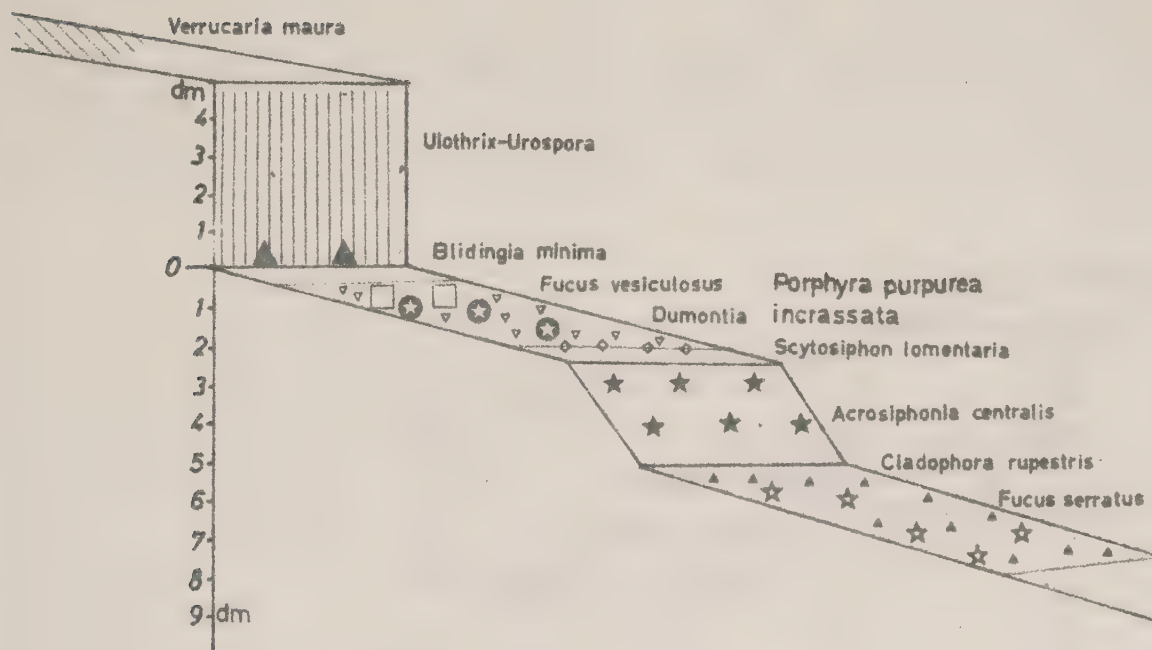


Fig. 134 F. Ransvik 13/6 1966.

Fig. 134 E - H. Ransvik 10/3 1964 13/6 1966 20/8 1965 1/11 1965.

The locality is situated ca 20 m from the above mentioned locality, substratum boulder, exposed from S-W and a little more sheltered, exposure index 3-4, inclination 90° to 20° . The same tendency as at the other locality at Ransvik concerning the changes in aspect is seen. The *Porphyra linearis* belt is here also gradually replaced by the *Ulothrix-Urospora* belt. Just below the 0-line there is a small but luxuriant belt of *Monostroma grevillei* in spring. This species has in recent years become more abundant and during March it covers the entire flat from 0 to -4 dm.

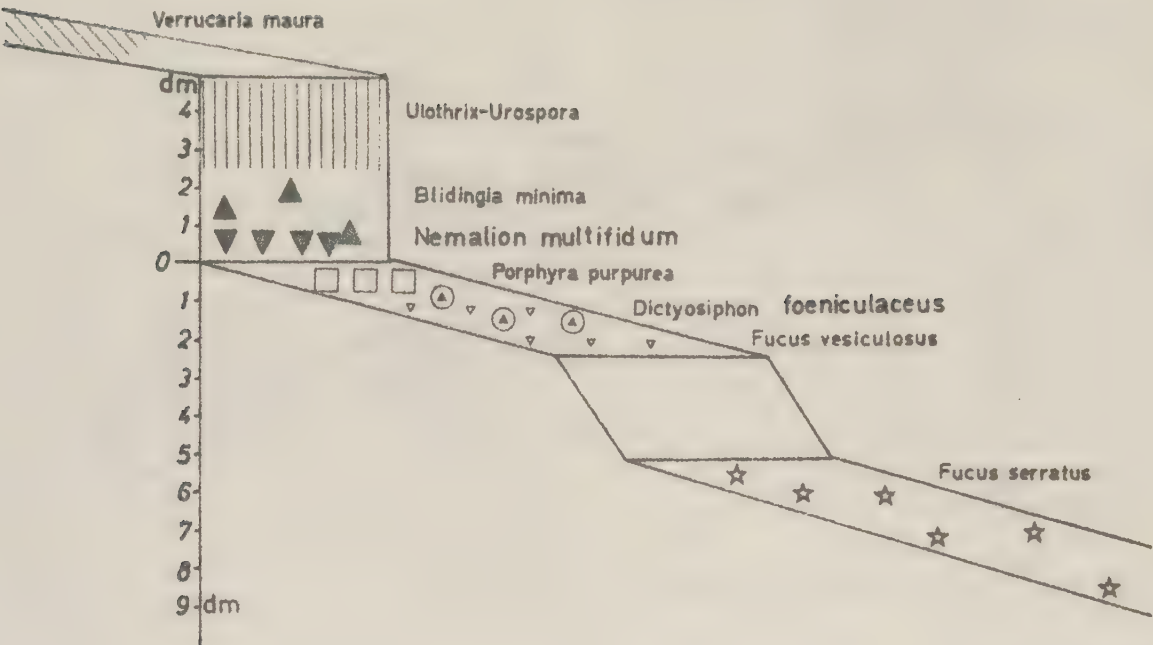


Fig. 134 G. Ransvik 20/8 1965.

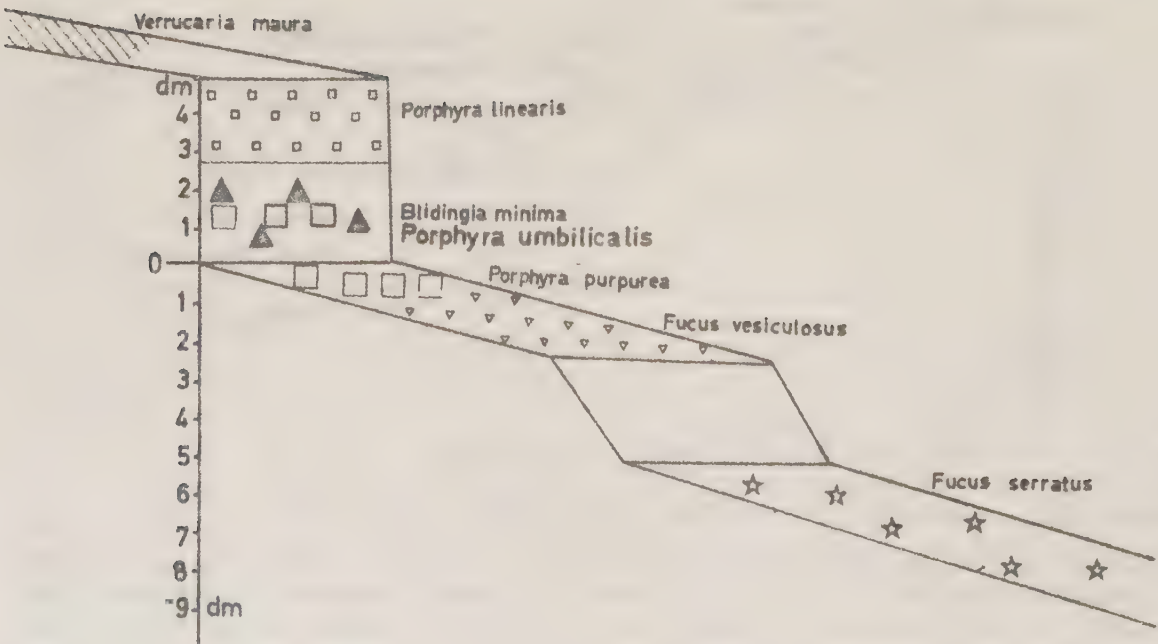


Fig. 134 H. Ransvik 1/11 1965.

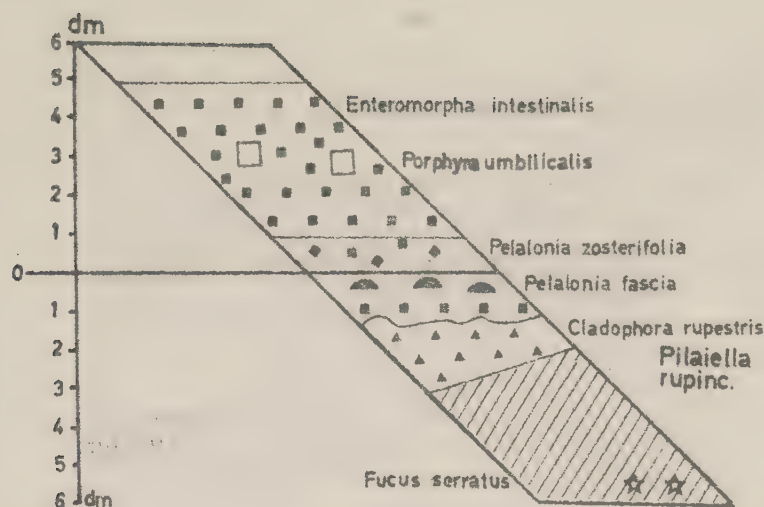


Fig. 135 A. Helsingborg 6/11 1966.

The locality is a jetty in the northern part of Helsingborg, substratum boulder, exposed from NW-SW, exposure index about 4-5, inclination about 30° . This vegetation profile could be compared with Ransvik 2/11 1966 (Fig. 134 D). Though the exposure index is about the same it is noticeable that the *Porphyra linearis* belt is completely lacking and has been replaced by a dense and luxurious belt of *Enteromorpha intestinalis* with some patches of *Porphyra umbilicalis*. Both the *Petalonia zosterifolia* and *fascia* belts are not so well developed as at Ransvik. The *Chordaria flagelliformis* belt is only represented by some single specimens and the *Polysiphonia urceolata* belt is replaced by a *Cladophora rupestris* belt. The *Pilaiella rupincola* belt is not found around the 0-line as at Kullen and Hallands Väderö but from about -4 dm and downwards.

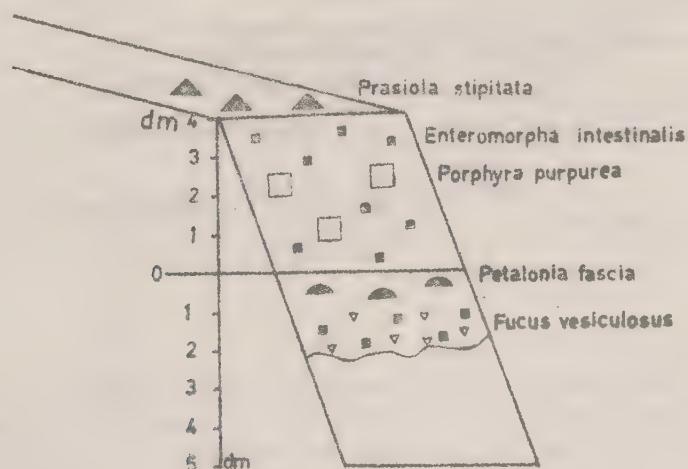


Fig. 135 B. Helsingborg 6/11 1966.

A more sheltered jetty in the neighbourhood of the above mentioned locality, substratum boulder, exposed from NW-SW, exposure index about 3, inclination $55-60^\circ$. The locality is also more polluted. The same tendency is seen as in Fig. 135 B, though the *Enteromorpha intestinalis* belt is not so dense. Note the *Prasiola stipitata* belt at +5 to +6 dm and the absence of *Petalonia zosterifolia*.

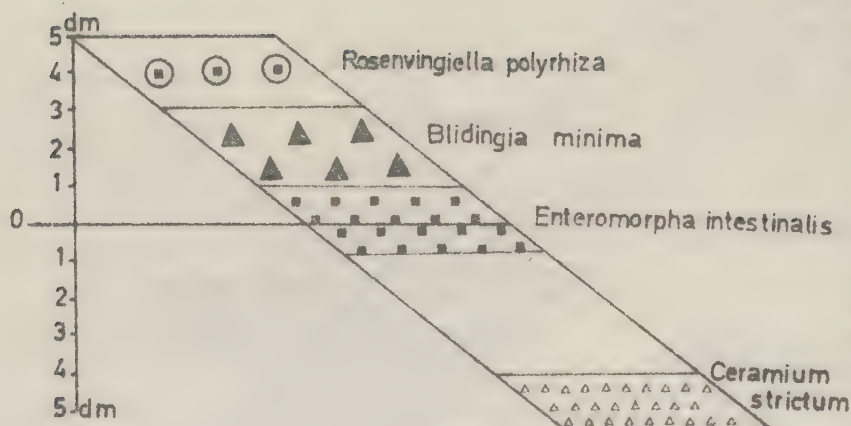


Fig. 136 A. Barsebäck 10/1 1969.

The locality lies on the northern side of the jetty of Barsebäck harbour, substratum boulder, exposed from NW-W, exposure index about 2, inclination 30-40°. The *Rosenvingiella polyrhiza* belt from +3 to +6 dm is in good condition. The *Enteromorpha intestinalis* belt extends from +1 to -1 dm. The zone from -1 to -4 dm is devoid of algae. Below -4 dm the *Ceramium strictum* belt is in rather bad condition.



Fig. 136 B. Barsebäck 20/5 1967.

Same locality as above. The *Rosenvingiella* belt extends from +4 to +8 dm, succeeded downward by a decaying *Blidingia minima* belt and an *Ulothrix-Urospora* belt between +2 dm and the 0-line. This could be compared with Kullen (Fig. 133 B) where at a very exposed locality the *Ulothrix-Urospora* belt is found from +1 to +6 m. Around the 0-line there is a very poor vegetation of *Scytosiphon lomentaria* and *Spongomorpha pallida*. The *Enteromorpha intestinalis* belt is restricted from -0.5 to -1.2 dm. The *Acrosiphonia centralis* belt is luxuriant and dense from -1.5 to -4 dm. At Kullen (Fig. 134 A) the belt is found at more exposed localities from -4 to -8 dm. Below -4 dm the *Ceramium strictum* belt is dominant. This belt dominates the range from -4 and -5 dm down to about 2 m in depth at the localities south of Barsebäck.

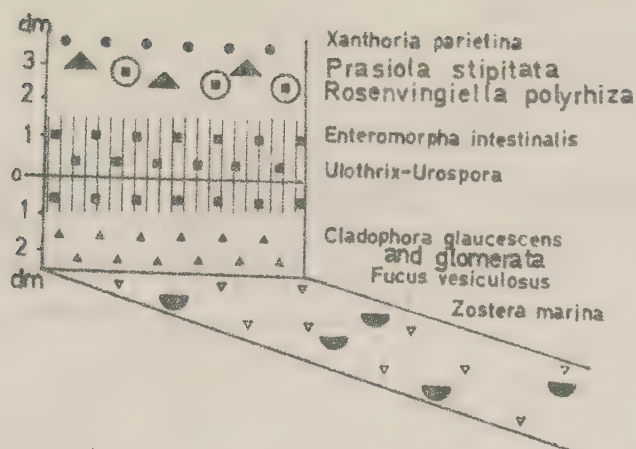


Fig. 136 C. Barsebäck 20/4 1968.

A locality south of the harbour, substratum boulders and below -2 dm sand and pebbles, exposed from S-SW, very sheltered, exposure index 0, inclination 90° and $10-20^{\circ}$. The *Xanthoria parietina* belt is found as low as +4 dm. *Prasiola stipitata* and *Rosenvingiella polyrhiza* are found in a narrow zone from about +2 to +3 dm. The *Ulothrix-Urospora* belt has here a vertical range of only 2.5 dm and is decaying. It is replaced by an *Enteromorpha* belt. From -1 to -3 dm there is a dense mixture of *Cladophora glaucescens* and *glomerata*. During recent years *Cladophora glomerata* seems to be the most dominant of the two species. On the sand below -3 dm there is a mixture of *Fucus vesiculosus* and *Zostera marina*. On this locality *Nemalion multifidum* is found in scattered specimens 2-4 cm in length near the 0-line in November.

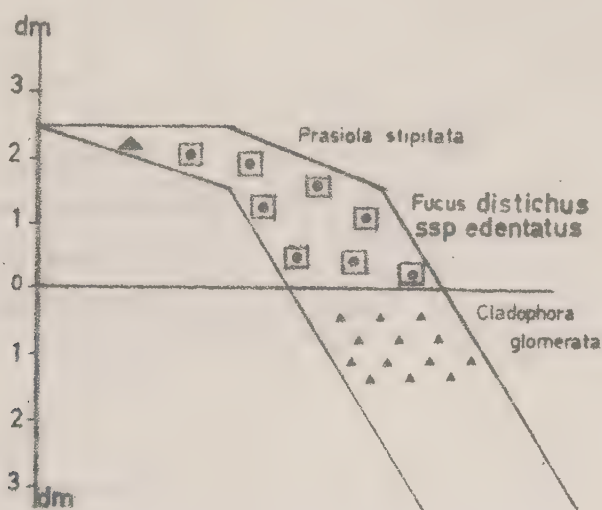


Fig. 137. Tre Kroner 23/3 1969.

The locality lies at the entrance to the harbour of Copenhagen. It is highly polluted, substratum boulder, exposed from SE-N, sheltered from waves but exposed to swell from boat traffic, inclination 10° and 50° . This vegetation profile is an example of an abnormal zonation. *Fucus distichus* ssp *edentatus* grows here above the 0-line instead of at -2 to -6 dm below. This is probably due to the constant swell from the boat traffic in the area. From the 0-line to -2 dm a dense belt of young stages of *Cladophora glomerata*. Below this zone no vegetation.

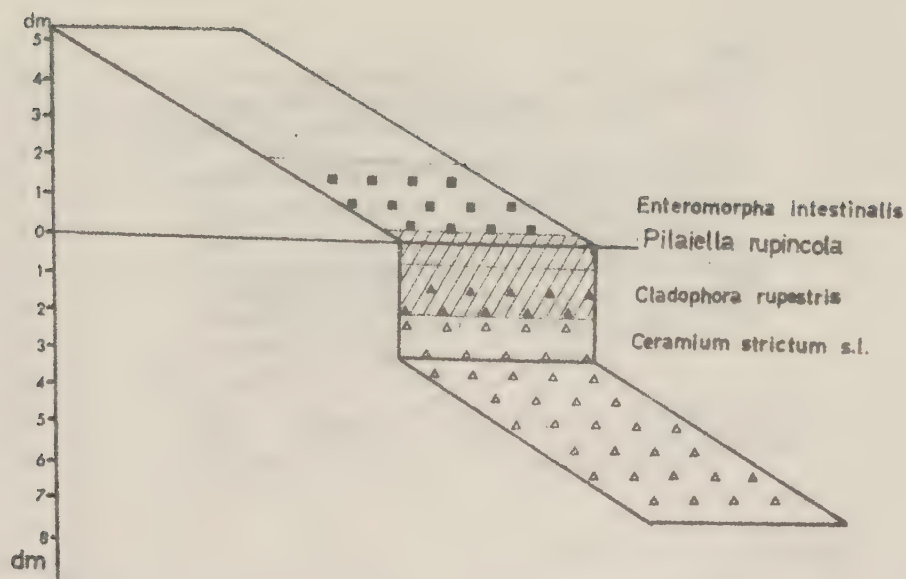


Fig. 138 A. Skanör 1/2 1967.

The locality lies on the northern jetty of the Skanör harbour, substratum boulder, exposed from N-W, exposure index about 3-4, inclination $30^{\circ} - 90^{\circ} - 20^{\circ}$. From the 0-line to +1.5 dm there is an *Enteromorpha intestinalis* belt in good condition. Below this from +0.25 to about -2 dm stretches a belt of young *Pilaiella rupicola*. In the lower part of this zone weak old specimens of *Cladophora rupestris* are found. From -2 to -8 dm there is a relatively dense carpet of old *Ceramium strictum/tenuicorne*.

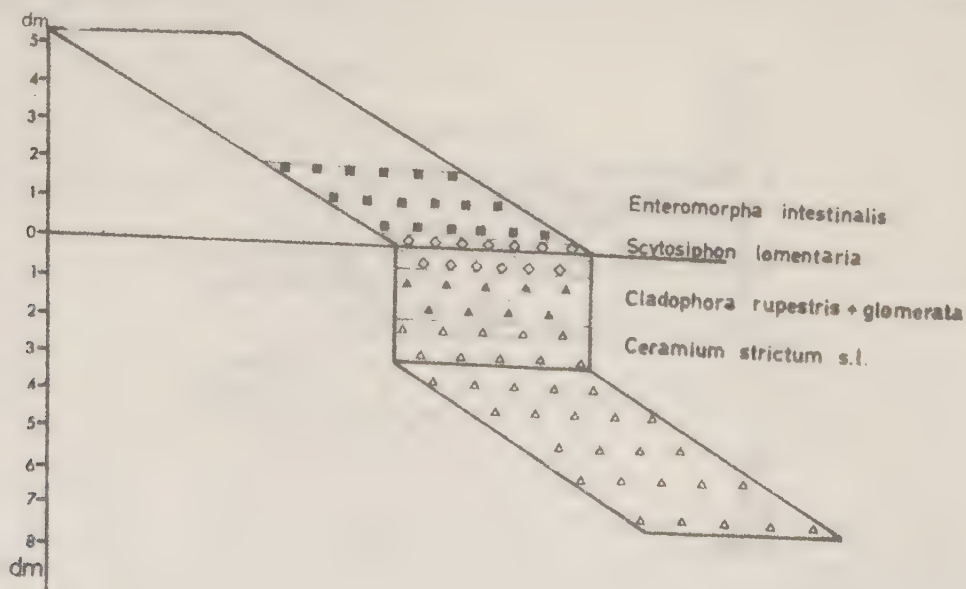


Fig. 138 B. Skanör 10/5 1967.

Same locality as above. The *Enteromorpha intestinalis* belt is renewed after the low water period and is now growing vigorously. Around the 0-line there is a narrow but distinct *Scytosiphon lomentaria* belt from +0.5 to -0.5 dm. In the upper part of the *Cladophora* belt from -0.5 to -2 dm there are a few specimens of *Acrosiphonia centralis*. *Cladophora rupestris* has retained its growth but is soon overgrown by *Cladophora glomerata*. The *Ceramium strictum/tenuicorne* belt is now luxuriant.

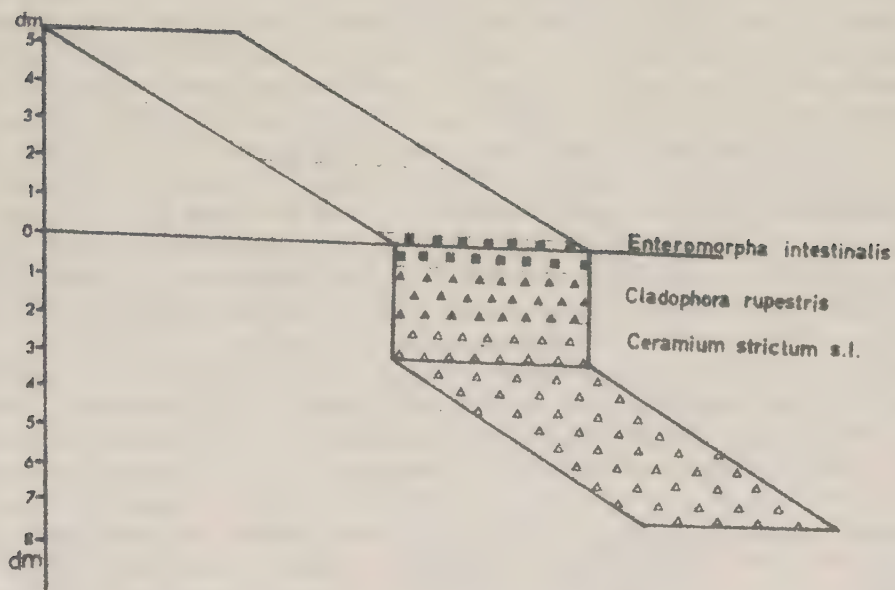


Fig. 138 C. Skanör 1/10 1966.

Same locality as above. A small belt of *Enteromorpha intestinalis* has begun to grow in the zone around the O-line. Here are also small patches of a weakly developed *Ulothrix-Urospora* belt. In the *Cladophora* belt the growth has ceased and nearly all *Cladophora glomerata* specimens are dead. The *Ceramium* belt is still in comparatively good condition.

INFLUENCE OF LOW OXYGEN CONDITIONS

Relatively low oxygen saturation values are found in the deeper parts of the Öresund area (p. 67) and the values seem to be lower today compared with measurements thirty years ago. The values in most parts of the area are not yet low enough to have any major effect on the algal flora.

The bad condition of the attached algal communities, which has been observed in certain localities during summer in connection with decaying abnormal masses of loose-lying specimens of *Ectocarpus* sp, *Pilayella* sp, *Desmarestia viridis* and *Cladophora glomerata*, may indicate that this is an effect of harmful oxygen deficit especially during night.

INFLUENCE OF TRACE ELEMENTS

Trace elements, such as cadmium, cobalt, copper, lead, nickel and zinc, occur in small amounts in sea-water and some of them are essential for algal growth. But when the content is increased by e.g. pollution, they can have toxic effects either alone or more pronouncedly when they appear two or more in combination. When the program for this investigation was drawn up, studies of the effect of trace metals on benthic algae in the Öresund area were included. However, it soon became evident that this part was too large and time-consuming a task to be made within the program. Therefore, the main part of this investigation was undertaken by B. Hägerhäll. The results have partly been published (Hägerhäll, 1973).

The increased load of trace metals in the Öresund (p. 97) may have the following influence on the benthic algal vegetation: disturbances of the growth of some species, which may ultimately lead to disappearance of them (p. 309) most probably by reduced ability to compete for space, and accumulation of metals in the algae, which can be harmful in higher trophic levels.

Hägerhäll (loc.cit.) has convincingly shown that an increased accumulation of trace metal ions in the water will give rise to an increased accumulation in the algae. The surplus uptake varies from species to species and may also vary with season. The maximum accumulation, however, is not found in areas with the greatest load but in areas with an intermediate metal load. At some localities in the Öresund concentrations of 100 times the normal values have been found in many species for some metals, e.g. cadmium, copper, lead and zinc. Even if the concentration of e.g. cadmium and lead in the water is very low, the occurrence of these metals is easily demonstrated in the algae. The affinity of the red algae to accumulate high amounts of cadmium and lead should be mentioned.

As the metal content in the water at a certain locality varies within a large range, the content of the metals in the benthic algae might instead be used as an indicator of the average load at the locality with the exception of heavily polluted areas. The danger of the trace element pollution is obvious, when the concentrations in higher trophic levels are considered.

CHANGES IN THE COMPOSITION OF THE ALGAL FLORA DURING THE TWENTIETH CENTURY

It is possible to get a relatively good picture of the changes during the twentieth century by means of literature references and herbarium specimens. When comparing older and recent lists of specimens one has to bear in mind that species, which have not been recorded in older lists, may very well have been present but overlooked. Also the different intensity and scheme of the investigations play an important role. After a careful examination of the material it may be possible in most cases to judge whether a species has disappeared or "invaded" the investigation area.

Species which have not been found in earlier investigations or have increased noticeably in number.

As can be seen in Table 31, 30 species have not been recorded for the area before. In some cases it can also be demonstrated that species have increased in abundance since earlier investigations. Most of the red algae, which have not been

Table 31. Species which have not been recorded from the Öresund area in earlier investigations or have noticeably increased in number.

Species not recorded before	Species increased in number
RHODOPHYTA	RHODOPHYTA
<i>Porphyridium marinum</i>	<i>Erythrocladia irregularis</i>
<i>Acrochaetium emergens</i>	<i>Erythrocladia subintegra</i>
<i>Acrochaetium gynandrum</i>	<i>Porphyropsis coccinea</i>
<i>Acrochaetium kylinii</i>	<i>Bangia fuscopurpurea</i>
<i>Actochaetium macula</i>	<i>Acrochaetium daviesii</i>
<i>Kylinia rosulata</i>	<i>Trailliella intricata</i>
<i>Cruoriopsis gracilis</i>	<i>Petrocelis hennedyi</i>
<i>Callithamnion bipinnatum</i>	<i>Cystoclonium purpureum</i>
<i>Ceramium pedicellatum</i>	<i>Dumontia incrassata</i>
<i>Ceramium penicillatum</i>	
<i>Ceramium rescisum</i>	
<i>Ceramium rubriforme</i>	
<i>Ceramium tenuicorne</i>	
<i>Polysiphonia brodiaei</i>	
PHAEOPHYTA	PHAEOPHYTA
<i>Microsyphar zosterae</i>	<i>Ectocarpus</i> sp.
<i>Streblonema immersum</i>	<i>Hecatonema diffusum</i>
<i>Myrionema corunnae</i>	<i>Pilayella littoralis</i>
<i>Myriotrichia claviformis</i>	<i>Pilayella rupincola</i>
<i>Sphacelaria caespitula</i>	<i>Petalonia fascia</i>
	<i>Petalonia zostericifolia</i>
	<i>Desmarestia viridis</i>
	<i>Fucus distichus</i> ssp <i>edentatus</i>
CHLOROPHYTA	CHLOROPHYTA
<i>Sykidion droebakense</i>	<i>Monostroma grevillei</i>
<i>Chlorochytrium inclusum</i>	<i>Ulvaria oxysperma</i>
<i>Ectochaete leptochaete</i>	<i>Blidingia minima</i>
<i>Entocladia tenuis</i>	<i>Prasiola stipitata</i>
<i>Eugomontia sacculata</i>	<i>Rosenvingiella polyrhiza</i>
<i>Phaeophila engleri</i>	<i>Cladophora glomerata</i>
<i>Pilinia rimosa</i>	<i>Acrosiphonia centralis</i>
<i>Tellamia contorta</i>	<i>Spongomorpha pallida</i>
<i>Cladophora pygmaea</i>	
<i>Derbesia marina</i>	
<i>Codium dichotomum</i>	

observed earlier, may have been overlooked but *Acrochaetium macula* may be a new-comer, since it is so frequent that Levring (1935) should not have overlooked it. *Trailliella intricata*, which reached the Scandinavian waters in the later part of the 19th century, did not appear in the Öresund proper until 1964.

Among the brown algae it is only *Fucus distichus* ssp *edentatus*, which without doubt has colonized the Öresund area and now become abundant. Of other species which have increased in abundance, *Ectocarpus* sp, *Pilayella* sp and *Desmarestia viridis* may be mentioned. Especially *Desmarestia viridis* was considered to be sparse by earlier investigators.

Of the green algae most of the species new for the area may have been overlooked due to their minor size. *Codium dichotomum*, which has immigrated into the Scandinavian waters during the 20th century, has only reached the north border of

the investigation area. *Monostroma grevillei*, *Ulvaria oxysperma*, *Prasiola stipitata*, *Rosenvingiella polyrhiza*, *Cladophora glomerata* and *Acrosiphonia centralis* are today very common in the area but were reported by Hylmö (1916) and Levring (1935) either from a few localities or in low numbers.

Species which have changed their distribution in negative directions.

Compared with older investigations 14 species have decreased in abundance and 10 species are now lacking (Table 32). A very large material of algae has been examined and in such cases, where the species have apparently decreased in number, special care has been taken to find them. The author is convinced that the collected material has given a fairly correct picture of the composition of the recent algal vegetation. In some cases the changes are easy to prove.

Table 32. Species now lacking in the Öresund area or notably decreased in number compared with earlier investigation.

Species now lacking	Species decreased in number
RHODOPHYTA	RHODOPHYTA
<i>Acrochaetium stillophorae</i>	<i>Acrochaetium moniliforme</i>
<i>Rhodophysema georgii</i>	
<i>Lithophyllum litorale</i>	
<i>Melobesia lejolisii</i>	
<i>Melobesia limitata</i>	
<i>Choreocolax odonthaliae</i>	
PHAEOPHYTA	PHAEOPHYTA
<i>Sphaerotrichia divaricata</i>	<i>Entonema effusum</i>
<i>Spermatochnus paradoxus</i>	<i>Myrionema magnusii</i>
<i>Sphacelaria plumosa</i>	<i>Eudesme virescens</i>
	<i>Stilophora rhizodes</i>
	<i>Scytosiphon lomentaria</i> (locally)
	<i>Sphacelaria cirrosa</i>
CHLOROPHYTA	CHLOROPHYTA
<i>Blastophysa rhizopus</i>	<i>Capsosiphon fulvescens</i>
	<i>Ulva lactuca</i>
	<i>Bolbocoleon piliferum</i>
	<i>Ectochaete wittrockii</i>
	<i>Entocladia perforans</i>
	<i>Epicladia flustrae</i>
	<i>Chaetomorpha linum</i>

Among the brown algae, which have disappeared from the area, *Spermatochnus paradoxus* can be mentioned. Lönnberg (1898) who surveyed the fauna in the Öresund area and also made notes of the flora, says (translated from Swedish by the present author): "at some localities most of the larger seaweeds from one to some metres in depth carry soft, fluttering plumes of *Spermatochnus paradoxus*". Levring and Sjöstedt (both personal communication) found large amounts of the species in the seaweed beds in the Lomma and Lundäkra Bays in August to September during the 1930s. The present author has only found some small specimens of *Spermatochnus paradoxus* on two occasions in 1966. Up to 1968 *Eudesme virescens* was a common algae of the spring vegetation, at least in the south and central part of the Öresund. From 1969 until now very few specimens have been observed.

In the case of *Ulva lactuca* Hylmö (1916) considered it to be common at Limhamn. Weibull (1919) states (translated from Swedish by the present author): "C. A. Agardh, who records several rare species of seaweed in his list of algae

from the Swedish west coast, does not mention this species. In Lomma Bay it has not been found in great numbers until lately. Lönnberg did not with certainty find the species during his investigations in the Sound in 1898 and 1899, but he supposed that he might have found a specimen at Limhamn. I myself did not find it until 1909, washed ashore together with other algae at Alnarps strand (Lomma Bay). During later years *Ulva lactuca* has increased tremendously and it dominates the algal flora around Malmö". From 1964 to 1968 the present author has found isolated specimens of *Ulva lactuca* at several localities but during the last few years it has only been found at one locality at the island of Ven.

About *Capsosiphon fulvescens* Hylmö (1916) writes "kommt in dem Sund ziemlich häufig vor. --- In Limhamn kommt sie an der Spitze der Aussenseite der Molen vor und ist der Brandung sehr ausgesetzt. --- Im Hafen von Barsebäck befand sie sich reichlich an Kalksteinen. --- Eine andere Form --- habe ich an sehr seichten Ufern gesehen, wo sie an Steinen und auf Rasenplaggen unter anderen Strandalgen wuchs". Simmons (1898) also recorded the species in the vicinity of Malmö and Levring (1935) found the species at Kullen. The present author has only found the species once. In the herbarium of the Botanical Museum in Lund there are collections of *Chaetomorpha linum* made by Hylmö from Kullen, Mölle and Barsebäck. Waern (1965 a) found the species west of Malmö but the author has only found a few specimens in the canal of Falsterbo.

About the decreased abundance of e.g. *Eudesme virescens*, *Spermatocnus paradoxus*, *Capsosiphon fulvescens*, *Ulva lactuca*, *Epicladia flustrae*, *Chaetomorpha linum* and *Blastophysa rhizopus* and the discontinuous distribution of *Scytosiphon lomentaria* along the Scanian coast, one can suspect some toxic effects, e.g. the observed increased level of trace metals.

The present author has observed how the number of species is markedly reduced in one area with a high load of trace elements in the vicinity of Helsingborg. From Fig. 139 it is evident that the number of species in the littoral and upper part of the sublittoral zone is reduced to only one (*Enteromorpha intestinalis*), where the concentration of copper is highest. At the same time the shores are covered with a film of diatoms instead of benthic algae. The breadth of this film expands as the number of benthic algae decreases.

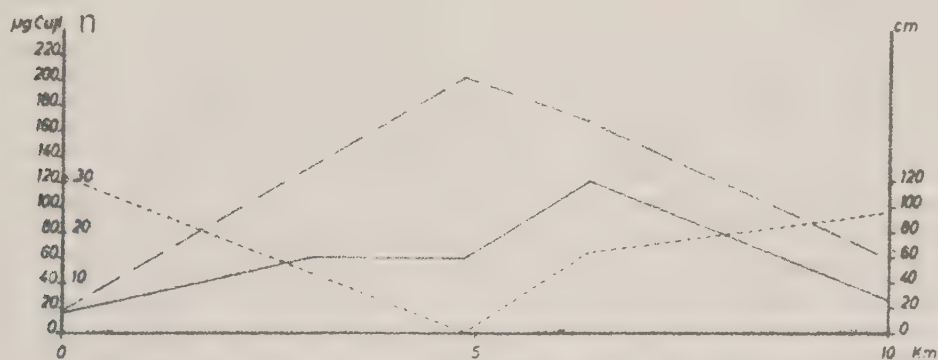


Fig. 139. The influence of high concentrations of Cu ions in the water on the number of benthic algal species and on the breadth of the diatom zone along the shore south of Helsingborg.

--- µg Cu/l number of benthic algal species
 ————— breadth in cm of the diatom zone

Kessler (1959) has observed that *Chaetomorpha linum* in culture is damaged at very low concentrations of copper in the medium. For *Ulva lactuca*, A. Kylin (1943) has shown that even small additions of copper, e.g. 2.5 $\mu\text{g/l}$, reduce the growth of juvenile stages by 50 % and an addition of 25 $\mu\text{g/l}$ kills the germlings. In mature specimens the lethal dose is somewhat higher. The toxicity also depends on salinity. Lower salinity apparently gives a lower resistance to toxic metal ions. Hägerhäll (1971) showed in culture studies of *Ulva lactuca* that the synergistic effect of two or more metal ions in combination drastically increases the toxicity. For example 3 $\mu\text{g/l}$ of copper and lead and 33 $\mu\text{g/l}$ of zinc have the same effect as 50 $\mu\text{g/l}$ of copper alone. In both cases the growth was reduced by 50 % compared with the controls.

However, one has to bear in mind that only free ions in the medium have a toxic effect. That the damage to the algal flora is not larger must depend on the chelating agents, which partly emanate from the sewage outlets and neutralize the output of toxic trace elements.

For species like i.a. *Rhodophysema georgii*, *Melobesia lejolisi*, *Myrionema magnusii* and *Entocladia perforans*, which belong to the *Zostera marina* flora, the decrease in abundance is probably due to the "Zostera disease", which killed almost all *Zostera* vegetation in Skagerack, Kattegatt and the Öresund in the middle of the 1930s. The *Zostera* vegetation did not recover until the middle of the 1940s.

EFFECTS OF INCREASED LEVEL OF NUTRIENT SALTS

The level of nutrient salts has without doubt increased in the Öresund area from the beginning of the thirties up till now due to increased pollution both from Sweden and Denmark and additions from Kattegatt and the Baltic. Compared with measurements in the thirties (Steemann Nielsen; 1937) the Öresund area has changed from a water poor in nutrient salts to a rather eutrophic water.

There is a well established correlation between algal growth and available nutrients, e.g. Ryther & Dunstan (1971) and Lindahl & Melin (1973). These studies have mainly been performed under laboratory conditions. There are very few if any in situ measurements of these phenomena and at least no previous measurements from the Swedish west coast in this field. It is, therefore, very hard to prove in figures that the production of benthic algae in the Öresund area really has increased. But according to the author's observations there are strong indications that this is the case.

During the last decades an increase in the biomass of certain species has been observed. This is especially the case for confervoid algae, such as *Ceramium* sp, *Polysiphonia* sp, *Ectocarpus* sp, *Pilayella* sp, *Desmarestia viridis*, *Monostroma grevillei*, *Ulvaria oxysperma*, *Enteromorpha intestinalis*, *Cladophora glomerata* and other *Cladophora* species. These species often become detached, when they reach a certain size and then drift along the bottom in large masses, especially in April to July. *Desmarestia viridis*, which in the beginning of the sixties was found in relatively low numbers, has since 1968 occurred in large quantities during May and June. As stated on p. 212, 30 - 40 % of the total biomass at depths from 10 - 25 m may consist of *Desmarestia viridis*. While trawling for fish from a research vessel west of Barsebäck at 15 - 20 m in depth in the beginning of May in 1968, the trawl was completely filled up in less than five minutes with *Ectocarpus* and *Pilayella* specimens floating along the bottom.

A part of these algal masses is also washed ashore and can generate large algal beds in shallow waters and on shores, causing sanitary problems. This secondary load will of course lead to an increased oxygen consumption both along the shore but most prominently in the deeper water layers.

Phosphorus and nitrogen content in algal material

The total phosphorus and nitrogen content in algal material from the Öresund has been estimated for some species. The material has been collected during the whole year from localities in the entire area, mainly Hallands Väderö, Kullen, Gilleleje, Hornbæk, Helsingborg, Barsebäck and Klagshamn.

Table 33. The total phosphorus and nitrogen content in different algal species...

Species	mg P/g dry weight			mg N/g dry weight			N/P
	Min.	$\bar{X}$	Max.	Min.	$\bar{X}$	Max.	
<i>Ahnfeltia plicata</i>	1.09	1.54	1.96	34.04	37.65	40.34	25.3
<i>Ascophyllum nodosum</i>	0.61	0.99	1.37	6.25	13.33	23.89	10.3
<i>Ceramium rubrum</i>	1.71	4.24	5.54	21.30	28.87	43.16	8.1
<i>Chondrus crispus</i>	1.75	1.90	2.22	21.94	24.56	26.33	12.9
<i>Ectocarpus confervoides</i> s.l.	0.82	1.06	1.29	15.30	18.77	22.24	18.0
<i>Fucus serratus</i>	0.57	2.01	5.06	10.25	19.20	29.80	9.6
<i>Fucus vesiculosus</i>	0.36	2.01	5.22	9.39	23.31	55.83	12.7
<i>Furcellaria fastigiata</i>	0.45	1.80	2.47	8.76	30.61	35.97	17.0
<i>Laminaria digitata</i>	2.06	2.31	2.56	13.00	17.43	21.68	7.6
<i>Phycodrys rubens</i>	0.30	0.77	1.24	20.68	25.93	35.40	48.7
<i>Phyllophora brodiaei</i>	0.64	1.06	1.78	15.31	30.88	46.12	29.1
<i>Polyides rotundus</i>	1.74	4.44	7.13	40.19	40.36	40.53	14.5
<i>Polysiphonia nigrescens</i>	0.76	0.96	1.11	21.95	29.84	41.96	14.6

Method: From each population about five samples were taken. The algae were dried to constant weight at 65 °C. Of each sample 2 - 5 parallel analyses of total phosphorus and nitrogen were made. The total phosphorus analyses were performed according to Andersson (1968) and the total nitrogen analyses according to Kjeldahl.

The results are shown in Table 33. There are large differences in the phosphorus and nitrogen content between the different species. There seems to be a tendency to higher nitrogen values for the red algae than for the brown algae. The values for the same species vary within a broad range probably depending on locality, depth and time of the year. The N/P ratio varies between about 8 and 49.

For *Fucus serratus* and *Fucus vesiculosus* comparative analyses were made on material from the Baltic (Blekinge) and from herbarium specimens collected at Hallands Väderö, Kullen and Barsebäck from 1900 to 1930 (Table 34). Comparison is also made with analyses on material collected in Lomma Bay by Weibull (1919). There are indications of an increased level of phosphorus and nitrogen, especially phosphorus, in both species of *Fucus* in the Öresund nowadays, compared with the conditions in the beginning of the 20th century. It does not seem probable that the phosphorus and nitrogen content of the herbarium specimens would have changed to a greater extent during storage. Concerning Weibull's measurements, it is noticeable that the nitrogen content in the algae was surprisingly high in spring. Lomma Bay was, however, already at that time influenced by urbane sewage from Malmö (cf. the bloom of *Ulva lactuca* p. 309). Even compared with Blekinge the recent values in the Öresund are higher.

The increased phosphorus and nitrogen accumulation in the algae in the Öresund, besides the increased production, will reduce the transport of these elements to Kattegatt and increase the recirculation within the area. This will probably also lead to a greater storage of phosphorus and nitrogen in the sediments.

Table 34. Comparison between the total phosphorus and nitrogen content in recent and older material of Fucus species.

Fucus serratus	mg P/g dry weight			mg N/g dry weight			N/P
	Min.	$\bar{X}$	Max.	Min.	$\bar{X}$	Max.	
Öresund 1900-1930 Herbarium specimens	0.39	1.10	1.30	8.29	15.54	17.75	14.1
Lomma Bay spring Weibull (1919)		1.2			28		23
" summer, autumn		0.9			11		13
Öresund 1972-74	0.57	2.01	5.06	10.25	19.20	29.80	9.6
Blekinge 1973	0.98	1.14	1.37	11.40	13.25	14.90	11.6
Fucus vesiculosus							
Öresund 1900-1930 Herbarium specimens	0.28	0.91	1.33	5.00	14.34	20.70	14.1
Lomma Bay spring Weibull (1919)		1.3			25		19
" summer, autumn		1.0			14		14
Öresund 1972-74	0.36	2.01	5.22	9.39	23.31	55.83	12.7
Blekinge 1973	1.11	1.39	1.91	11.60	13.46	15.40	9.6

Estimation of biomass

It is essential to know the biomass of benthic algae in combination with i.a. the amount of phosphorus and nitrogen bound in algae, for estimating the production and making budgets of the inflow and outflow of nutrient salts in an area. The intention is to make a survey of the total algal biomass for the entire Öresund area in the future. It may be of some use to give a brief description of the present results.

Method: To collect the algae a quadrangular frame with an area of 0.25 m² was placed on the bottom on every metre from the 0-line to 15 m in depth. By a SCUBA-diver all the algae within the frame were removed and taken to the laboratory for assortment and removal of animals. Then they were dried to constant weight at 105 °C.

The biomass of the benthic algae has been estimated for two localities, Kullen in the northern part and west of Klagshamn in the southern part of the area (Table 35). To get a better understanding of the values from the southern part of the Öresund some measurements from the Baltic proper (Pukavik, Blekinge) were performed. When evaluating the figures one has to bear in mind that there is of course a great variation in weight/area, depending of locality and season of the year. The figures from the southern part of the Öresund are lower than at Kullen and in Blekinge, at least down to 5 m in depth. The highest value found in the Fucus zone west of Klagshamn was 860 g/m². The low values for 9-11 m in Blekinge probably depends both on poor light conditions due to high turbidity and on lack of suitable substratum (sand with pebbles).

A possible explanation to the lower biomass in the southern part of the Öresund may be the heavy fluctuations of salinity in this area. This is also proposed

Table 35. The biomass of benthic algae as dry weight in g/m^2 at different depths and localities.

Mean values of five (Kullen) or ten (W. Klagshamn, Pukavik) samples from each depth.

Depth in m	Kullen	W. Klagshamn	Pukavik
0 - 1	2110	350	1400
1 - 2	680	70	(1-3) m 1820
2 - 3	690	-	
3 - 4	170	-	(3-5) m 150
4 - 5	190	30	
5 - 6	230	-	-
6 - 7	180	-	-
7 - 8	45	55	-
8 - 9	50		-
9 - 10	45		(9-11) m 25
10 - 11	150		
11 - 12	150	1 = measurements in the Laminaria belt	
12 - 13	105	The values from Kullen are obtained from Kornfeldt (1973) except at 0-2 m and in the Laminaria belt at 14-15 m in depth.	
13 - 14	160		
14 - 15	95,240 ¹		
15 - 16	80		

by Lund (1936), who measured the growth of *Fucus vesiculosus* at Saltholm. It is also noticeable that low values are obtained at Kullen at 7 - 10 m in depth. This may be induced by the fluctuating salinity in the depth where the halocline oscillates.

Special interest has been paid to the variation in biomass of the *Fucus* zone at Kullen. During spring 1973 samples were taken in the *Fucus* zone on one occasion in each of February, March and May. The samples were collected from one locality within a distance of 100 m, so that differences in exposure and other environmental factors were as small as possible. The sampling places were randomized by throwing the frame in the *Fucus* zone. On each occasion five parallel samples were taken. All epiphytes were removed and treated separately. The variation in biomass of the *Fucus* zone may be comparatively great (Table 36). The main components of the epiphyte flora were *Ectocarpus confervoides* s.l., *Elachista fucicola* and *Pilayella littoralis*. The dry weight of the epiphyte fraction varied from 9 g/m^2 at the beginning of March to 98 g/m^2 at the end of May.

Some other measurements of the biomass of the *Fucus* zone at Kullen during the same period gave indication that the average biomass decreases with increasing degree of exposure.

Table 36. The biomass of the *Fucus* zone as dry weight in g/m^2 at Kullen.

February			March			May		
Min.	$\bar{X}$	Max.	Min.	$\bar{X}$	Max.	Min.	$\bar{X}$	Max.
180	730	1160	1240	1430	1570	930	1370	1970
			1290 ¹	2110 ¹	3570 ¹			
			1 = Ascophyllum zone					

Factors limiting the growth of the algae

It has become a matter of great interest during recent years to determine limiting nutrient factors for the algal growth in eutrophic waters. For this purpose the ratio N/P has generally been used. In the literature one can find the N/P ratio expressed either as total-N/total-P or inorganic-N/inorganic-P. In the first case the figures are not relevant if the rate of release of inorganic compounds is unknown. As N-NO_3 , N-NO_2 , N-NH_4 and smaller organic nitrogen compounds, such as amino acids, can be utilized by the algae (Fries, 1973), the ratio between available nitrogen and P-PO_4 seems to be the most useful. It has been suggested by several authors, e.g. Gargas (1972), that if the ratio available nitrogen/ P-PO_4 is less than 7, nitrogen is the limiting factor and if the ratio is more than 7, phosphorus is the limiting element. If the ratio is around 7, anyone of the elements could be limiting. This, however, may be true only if the concentration of the nutrient salts is comparatively low. The surplus uptake of phosphorus by the algae must also be considered (cf. Nyholm, 1974).

The ratio available-N/ P-PO_4 has been calculated for the nutrient salt measurements in the Öresund area (p. 71 and following). The ratios vary from 0.5 to 60. To elucidate the variation the material was arranged chronologically. It was then found that there is a strong tendency to dominating high values from January to April. During the period May-August low values are in the majority. In the period September-December low and intermediate values are most prominent.

To illustrate the conditions in the area during one year two localities have been chosen, east of Hornbæk in the northern part and Kalkgrundet in the southern part. The results are given in Figs. 140 and 141. There are variations between different depths, but at least at Kalkgrundet the trend of the different depths is similar. In the northern part of the area the variation is somewhat more complicated, e.g. at 15 m in depth. Generally, however, it can be said that low values are found in summer. As there is a tendency to decreasing amount of available nitrogen during this time of the year, it may be possible that nitrogen governs the growth of phytoplankton and the benthic algae more during summer than the rest of the year.

The role of phosphorus as a limiting factor might be more disputable. Neither of the elements may have any influence on the production of the algae, as in many cases the content in the water is comparatively high. The possibility that other ions can act as limiting factors must always be considered, e.g. cobalt, copper, iron and zinc (cf. Lindahl & Melin, 1973), but as stated on p. 97 the amount of trace elements is high enough in the area. For greater depths and during winter-time the light conditions may without doubt be a limiting factor.

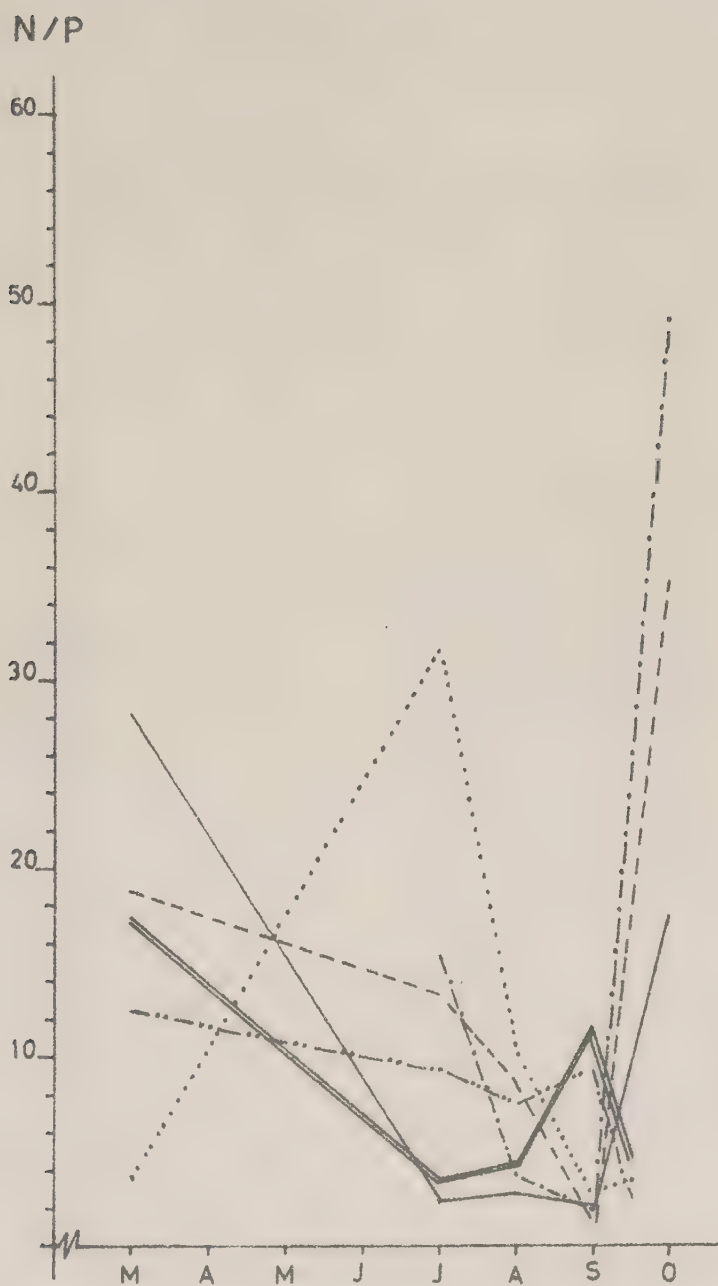


Fig. 140. N/P-ratio ($\text{N-NO}_3 + \text{N-NO}_2 + \text{N-NH}_4 / \text{P-PO}_4$) at different depths east of Hornbaek in 1973.

— 0 m - - - 5 m - · - · - 10 m
 · · · · · 15 m - · - · - 20 m — 25 m

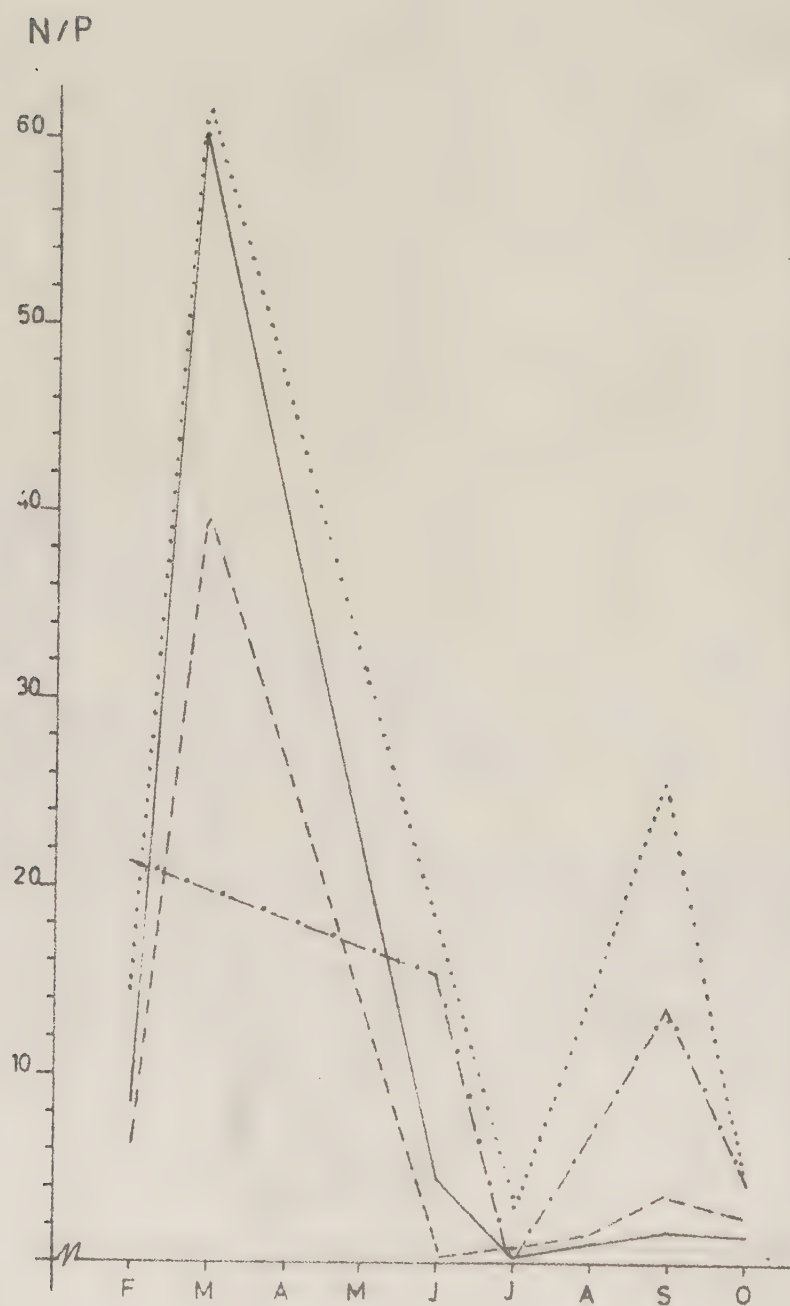


Fig. 141. N/P-ratio ($\text{N-NO}_3 + \text{N-NO}_2 + \text{N-NH}_4 / \text{P-PO}_4$) at different depths at Kalkgrundet in 1973.

————— 0 m - - - - - 2.5 m
 - 5 m 10 m

PHYTOGEOGRAPHICAL CLASSIFICATION OF THE ALGAL FLORA

Lönnberg (1898) considered the flora of the Öresund to give "a high boreal impression". Rosenvinge (1935) surveyed the phytogeographical conditions of the red algae in Danish waters. He found among the red algae with south borders in the Öresund area three subarctic, three boreal-arctic, five cold-boreal and ten warm-boreal species. Waern (1965 a) says "the vegetation has a touch of arctic character".

In order to encompass the phytogeographical situation in the Öresund area the author has mainly used the classical system of Börgesen & Jónsson (1905) with some additions by Levring (1940) and Lund (1959 b). When doing this one has to bear in mind that Börgesen & Jónsson's lists are incomplete and the known distribution for many species has expanded due to new finds. In some cases the species delimitation has changed. Some species which are not mentioned in the lists have been grouped according to the distribution given by Pankow (1971). The following species from the Öresund area have not been included in the calculations, as their distribution is poorly known:

RHODOPHYTA

Porphyridium marinum
Erythrocladia irregularis
Erythrocladia subintegra
Porphyra purpurea
Acrochaetium collopodum
Acrochaetium cytophagum
Acrochaetium dumontiae
Acrochaetium emergens
Acrochaetium gynandrum
Acrochaetium kylinii
Acrochaetium kylinioides
Acrochaetium macula
Acrochaetium moniliforme
Acrochaetium pectinatum
Acrochaetium polyblastum
Acrochaetium reductum
Acrochaetium strictum
Acrochaetium thuretii
Kylinia rosulata
Cruoriopsis gracilis
Lithothamnion granii
Callithamnion bipinnatum
Ceramium areschougii
Ceramium pedicellatum
Ceramium penicillatum
Ceramium rescisum
Ceramium rubriforme
Ceramium tenuicorne

Polysiphonia fibrillosa
Polysiphonia haemisphaerica
Rhodomela virgata

PHAEOPHYTA

Ectocarpus confervoides f. *hiemalis*
Ectocarpus confervoides f. *pygmaea*
Microsyphar porphyrae
Streblonema immersum
Ralfsia bornetii
Ralfsia clavata
Ralfsia lucida
Hecatonema diffusum
Myriactula fucorum
Sphacelaria plumigera

CHLOROPHYTA

Sykidion droebakense
Prasinocladus lubricus
Enteromorpha ahlneriana
Entocladia tenuis
Eugomontia sacculata
Phaeophila engleri
Tellamia contorta
Cladophora flexuosa
Cladophora fracta
Cladophora glomerata
Cladophora pygmaea
Codium dichotomum

The algal species in the Öresund area are rather evenly distributed between the different phytogeographical groups with some predominance for the cold-boreal group (Table 37). Among the red algae the cold-boreal and warm-boreal species are in the majority. There are few warm-boreal brown algal species. Among the green algae the subarctic and boreal arctic dominate.

When comparing the figures for Bohuslän, Öresund and Blekinge, it is evident that the number of warm-boreal species decreases markedly along the Swedish coast from Bohuslän to Blekinge, from 80 to 16. This reduction is found mainly for the red algae, both between Bohuslän and the Öresund (24) and from the Öresund to Ble-

Table 37. Phytogeographical classification of the algal flora in the Öresund compared with Bohuslän (Kylin, 1944, 1947, 1949) and Blekinge (Levring, 1940).

Number of species in the different groups are given.

a = arctic sa = subarctic ba = boreal-arctic cb = cold-boreal

wb = warm-boreal

		a	sa	ba	cb	wb
	Bohuslän	-	52	37	66	80
	Öresund	-	41	36	55	80
	Blekinge	-	26	29	34	16
Bohuslän	Rhodophyta	-	12	10	26	47
	Phaeophyta	-	23	12	29	25
	Chlorophyta	-	17	15	11	8
Öresund	Rhodophyta	-	12	10	25	23
	Phaeophyta	-	15	12	21	8
	Chlorophyta	-	14	14	9	8
Blekinge	Rhodophyta	-	4	6	13	5
	Phaeophyta	-	11	9	12	5
	Chlorophyta	-	11	14	9	6

kinge mainly within the Öresund (18) but also for the brown algae between Bohuslän and the Öresund (17). Also the cold-boreal and subarctic species diminish in number to the greatest part within the Öresund area. Within the boreal-arctic group the differences between the areas are small. The green algae seem to be the least affected within all phytogeographical groups.

The main conclusion might be that the warm-boreal species are the most sensitive to changes in the environment and the boreal-arctic the least. As shown on p. 37, the temperature conditions are relatively uniform in the entire area from Bohuslän to the Baltic. It is, therefore, supposed to be the decreasing and fluctuating salinity that determines the changes in the floral composition in the Öresund area also from the phytogeographical point of view.

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